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Digest

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Digest: Phenotypic plasticity and the genomic signature of novel castes: insights from soldier evolution in *Cephalotes*

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Abstract

Phenotypic plasticity can alter evolutionary dynamics, but its genomic consequences remain contested. Barkdull & Moreau (2026) combine comparative genomics and developmental transcriptomics in *Cephalotes* turtle ants to show that the repeated evolution of a soldier morph produces an asymmetric genomic signature: protein-coding genes experience genome-wide relaxed selection and reduced positive selection, whereas conserved noncoding regulatory elements show increased purifying constraint. Worker morph plasticity is driven mainly by co-option of ancient genes and by integration of insulin, imaginal-disc, and Hippo signaling.

Phenotypic plasticity, the ability of a single genome to produce discrete phenotypes depending on developmental cues (Sakamoto & Innan, 2024; Sommer, 2020), poses a paradox for evolutionary biology. Plastic systems can both expose and hide genetic variation from selection, with consequences for rates of molecular evolution (Espinosa-Soto et al., 2011; Gibert et al., 2019; Romero-Mujalli et al., 2024). Turtle ants (*Cephalotes*) provide a compelling natural experiment: many species produce two discrete worker morphs (small minor workers and large, armored soldiers) through developmental plasticity. Barkdull & Moreau (2026) integrate whole genomes from six *Cephalotes* species with time-series transcriptomes and comparative genomic analyses to test whether plasticity influences selection on coding genes and regulatory elements.

The authors assembled five new *Cephalotes* genomes and paired them with the published genome of *C. varians* (Smith, F., 1876), generating three phylogenetically matched pairs of polyphenic (soldier-producing) and monomorphic species. First, the authors inferred the evolutionary history of worker plasticity in the genus using ancestral-state reconstruction analyses. The authors then examined evolutionary pressures on thousands of protein-coding genes using a codon-model framework that distinguishes relaxed from intensified selection, and tested for evidence of positive selection. In parallel, they identified conserved noncoding elements and quantified their evolutionary rates relative to a neutral model, treating those as proxies for regulatory loci. Finally, the authors used transcriptomes from pupal and adult morphs to identify morph-biased genes, estimate gene ages through phylostratigraphy, and test for overlap with selective regimes and regulatory patterns. Figure 1 summarizes this workflow and the main results.

The analyses revealed a striking asymmetry. Across the genome, soldier-producing lineages showed a substantial shift toward relaxed selection on protein-coding genes: 12.3% of genes exhibited evidence of relaxed selection, compared to only 9.2% that evolved under intensified selection. There was also a reduction in positive selection: 2.6% of genes experienced positive selection in species which produce a solider, compared to 8.3% that were under positive selection in species lacking soldiers. These findings indicate that plasticity may buffer coding sequences from strong directional pressures. Genes differentially expressed between soldiers and minor workers were also not enriched for positive selection, challenging the expectation that morph-biased genes accumulate adaptive changes. Noticeably, regulatory DNA appeared to be under much tighter constraint in plastic lineages. The authors identified conserved noncoding elements, which likely function as regulatory loci, and found that far fewer of these elements evolve faster than neutral expectation in soldier-bearing species. Instead, most noncoding elements seem subject to purifying selection. This pattern indicates that the regulatory architecture underlying caste determination is strongly conserved, acting as an evolutionary "anchor" that maintains developmental fidelity.

To probe the evolutionary age of these morph-biased loci, the authors employed phylostratigraphy, an approach that infers the evolutionary origin of genes based on their phylogenetic emergence and conserved functional associations across extant organisms (Domazet-Lošo et al., 2007, 2017). They discovered that genes differentially expressed between castes are markedly older, being significantly overrepresented in deep evolutionary strata (e.g., Eumetazoa or earlier), and depleted of lineage-specific, younger genes. This result strongly indicates that the evolution of the soldier

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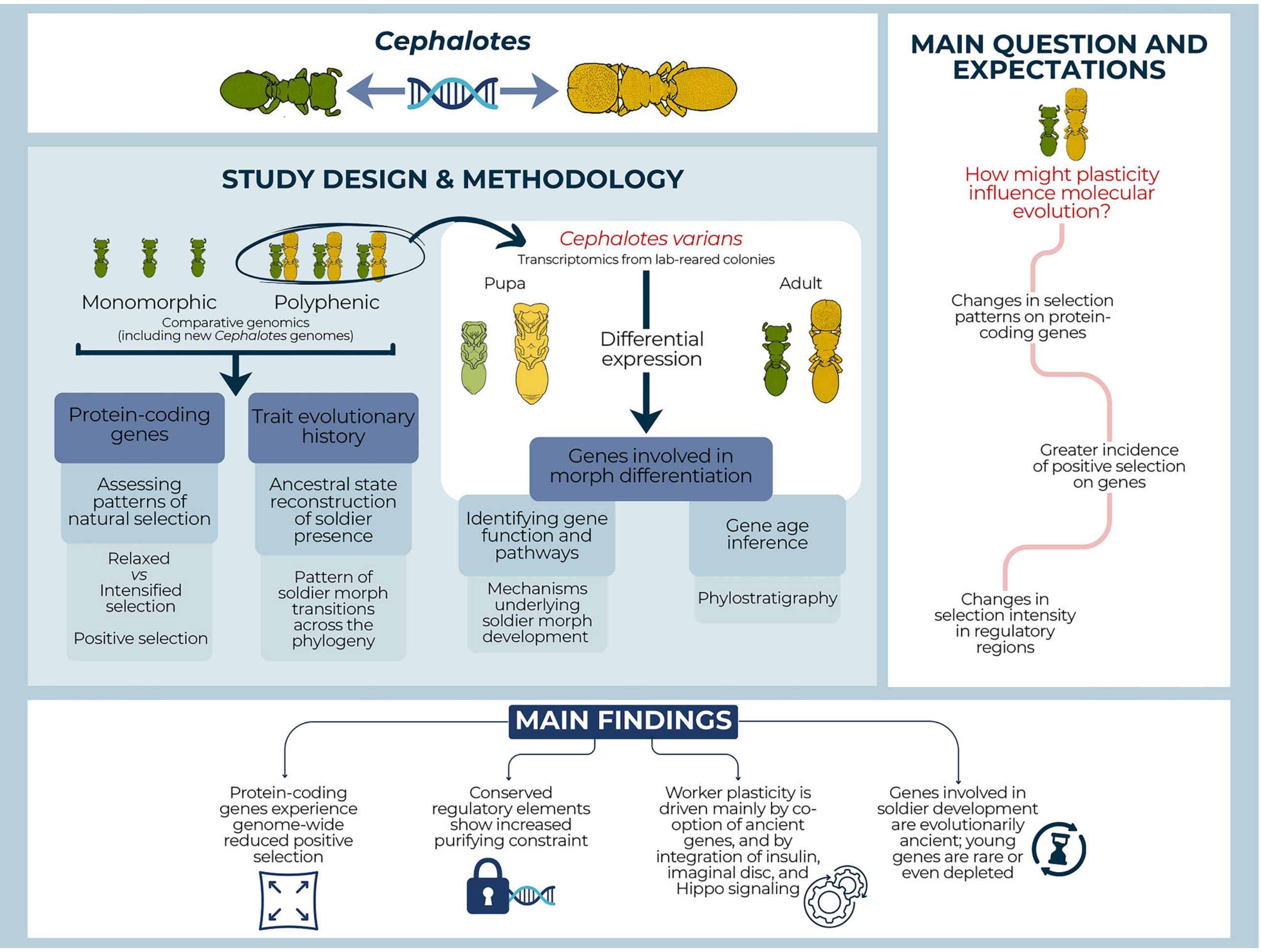

Figure 1. Study design and integrative analyses of molecular evolution associated with repeated soldier evolution in *Cephalotes*. Comparative genomic analyses were conducted across monomorphic and polyphenic species pairs to assess patterns of natural selection on protein-coding genes and reconstruct the evolutionary history of soldier presence. Developmental transcriptomics from *Cephalotes varians* were used to identify morph-biased genes, infer gene ages, and uncover pathways underlying soldier differentiation. The authors expected plasticity to generate contrasting evolutionary signatures across genomic compartments, and the results supported this prediction: protein-coding genes showed genome-wide relaxed and reduced positive selection, whereas conserved regulatory elements exhibited increased purifying constraint. Ant icons were adapted from the original article (Barkdull & Moreau, 2026).

phenotype largely relies on the co-option of ancient, conserved genes, rather than the recruitment of novel or fast-evolving ones. Ancestral-state reconstruction further indicates that the clade ancestor likely lacked soldiers. Moreover, analyzed transcriptomes showed that insulin-signaling and nutritional pathways were strongly enriched among morph-biased genes, likely directly linking larval nutritional inputs to caste fate. Differential gene expression associated with imaginal-disc development was also detected, supporting the idea that caste diversity is driven by modifications in conserved developmental modules. Critically, the results implicate the Hippo signaling pathway (Zhong et al., 2024) for the first time in eusocial insect polyphenism, identifying 22 caste-biased genes in this pathway. Because the Hippo pathway integrates signals from nutrition and growth, its involvement provides a plausible developmental mechanism for producing two discrete morphs from a shared genome.

Together, these findings support a simple but powerful conceptual model: plasticity relaxes selection on protein-coding genes (acting as a shield), while imposing purifying selection on regulatory elements (acting as an anchor). The repeated evolution of the soldier morph in *Cephalotes* thus reshapes the genome in a predictable, asymmetric way: coding regions can diversify, so long as the regulatory logic that ensures morph fidelity remains strictly conserved. From a broader evolutionary perspective, this means that phenotypic plasticity can decouple selective pressures across genomic elements and repeatedly mobilize conserved developmental circuits to generate novel phenotypes. The lack of elevated positive selection among morph-biased genes further supports the conclusion that phenotypic novelty arises mainly through regulatory redeployment of ancient pathways, a pattern consistent with other polyphenic systems (Corona et al., 2016; Muschick et al., 2011; Ogawa & Miura, 2014).

The shield-and-anchor model proposed by Barkdull & Moreau (2026) therefore provides a tractable framework for understanding how plasticity shapes genomic evolution. Future work combining developmental transcriptomes, population-level analyses of regulatory variation, and functional assays of candidate loci will be essential to test the model directly. Broader comparative studies across polyphenic taxa will clarify whether this asymmetric genomic signature is a general outcome of plastic development or a lineage-specific feature of *Cephalotes*.

Conflict of interest

The authors declare no conflict of interest.

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