

Genome architecture and social evolution

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A fundamental challenge in biology is explaining the evolution of novel phenotypes such as the origins of eusocial behavior. Eusociality—defined by overlapping generations, reproductive division of labor, and cooperative brood care (1)—has evolved at least 17 times in arthropods (2): widespread in the social Hymenoptera (ants, bees, and wasps) and observed in other orders (aphids, ambrosia beetles, termites, thrips, and snapping shrimp; Fig. 1). Although it has been remarkably successful for some lineages, eusociality remains rare in nature and has been repeatedly lost in other lineages (aphids and bees), suggesting that there may be major barriers to its evolutionary emergence (3). It is well appreciated that eusocial organisms arose from solitary ancestors, and phylogenetic treatments support the notion that social complexity evolved through prolonged parental care, mutual tolerance, and cooperative breeding (4). While the ecological, behavioral, and theoretical genetic drivers of eusociality have long been studied (5), analyses of the molecular genomic mechanisms that give rise to social complexity are in their infancy. The study of social arthropod genomics has revealed the basic genome size and chromosome composition across numerous taxa, but understanding their architecture and regulatory networks remains unclear.

One major outstanding question is the relative role of genome size and architecture as a cause or consequence of social complexity. Genomes are fluid in composition and vary in size and structure over time (6). In general, organisms with larger genomes tend to have more genes, introns, and transposable elements (TEs) than those with smaller genomes, but there are many exceptions. Notably, comparative studies in ants and bees suggest that there is no relationship between genome size and the evolutionary origins of eusociality or elaborations of social complexity (7, 8). In PNAS, Chak et al. (9) show that genome size scales with social complexity across 33 species and four independent origins of

Current genomic resources for eusocial arthropod species:

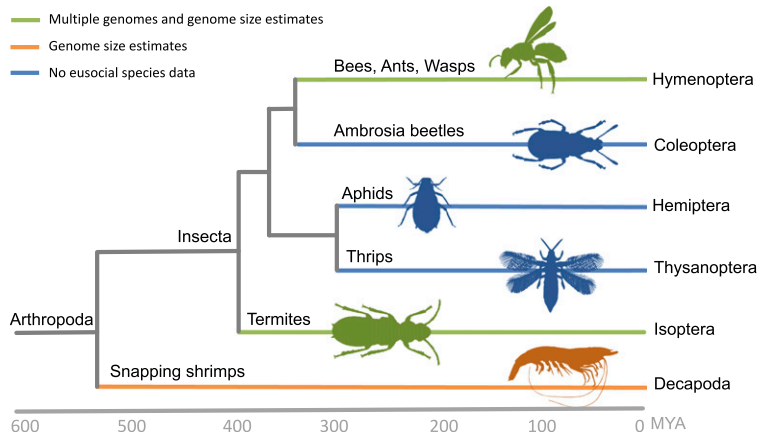


Fig. 1. Phylogeny of eusocial arthropod lineages. While social Hymenoptera and termites have relatively small genomes and a diverse set of genomic resources, and are increasingly well studied, other social insect lineages remain underrepresented, including snapping shrimps, thrips, aphids, and ambrosia beetles. In PNAS, Chak et al. (9) compare snapping shrimp genome sizes and TE estimates, an important first step toward understanding this independent origin of eusociality. Silhouette images credit: Phylopic. Bee image credit: Melissa Broussard, licensed under CC BY 3.0. Beetle image credit: T. Michael Keesey. Termite image credit: JCGiron, licensed under CC BY 3.0. Aphid, thrips and shrimp images credit: Christoph Schomburg.

eusociality in snapping shrimp, and they explore the relative contributions of TEs to account for expanded genome sizes.

TEs are mobile DNA that can lead to cut and paste mutations and copy and paste genome size expansions and rearrangements. TEs are of great interest for the study of behavioral genomics, and genome evolution more broadly, as they are known to reduce recombination (10), carry transcription factors which can lead to accumulation of *cis*-regulatory complexity (11), and generate adaptive phenotypes (12). Studies in obligately eusocial termites found that TEs comprise 10% of their genomes (13), but Chak et al. (9) show that, across a social spectrum of pair living to eusociality in snapping shrimp

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Author contributions: S.M.R. wrote the paper.

The author declares no competing interest.

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See companion article, "Eusociality in snapping shrimps is associated with larger genomes and an accumulation of transposable elements," [10.1073/pnas.2025051118](https://doi.org/10.1073/pnas.2025051118).

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Published July 2, 2021.

species, TE proportions shift from less than 1% to over 11%, respectively. While studies of termites and snapping shrimps indicate a possible relationship between genome size and TEs, these patterns do not hold across all arthropods. Some obligately eusocial Hymenoptera have greatly reduced TE composition; for example, TEs comprise only 3% of the advanced eusocial honey bee genome (7, 14). Moreover, these numbers vary widely among Hymenoptera: TEs comprise 6 to 50% of eusocial ant genomes (15, 16), but studies on solitary *Nasonia* wasps also reveal a large proportion of TEs (20%) in their genome (17). The adaptive significance TEs contribute to behavioral genomics and social evolution therefore remains unclear, as each independent origin of eusociality may converge on similar phenotypes via disparate molecular mechanisms (18). Ultimately, additional phylogenetically informed analyses of genome size, architecture, and gene regulatory network data are needed to address this question. As sequencing costs are ever declining, researchers can foreseeably sequence and analyze more social arthropod genomes, adding the so far understudied eusocial snapping shrimp, aphids, thrips, and ambrosia beetles (Fig. 1). With these genomic tools in place, this will set the stage for associated epigenetic studies of social phenotypes to bridge

the gap to examine the relationship of genome architecture and eusocial traits.

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With new nonmodel systems and additional resources emerging at an exponential rate (19), it is truly an exciting time to be studying behavioral genomics. Although the genomic consequences of living in complex societies have been studied in termites (13), and across eusocial Hymenoptera (7, 8, 15), important comparative insights can be gained from looking outside of obligately eusocial taxa to include solitary and simple societies (20). Moving forward, further studies like Chak et al. (9) are essential to explore the relationship between independent origins of eusociality and genome architecture across the spectrum of additional group living and eusocial species.

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