

# Climbing the social ladder: the molecular evolution of sociality

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**Genomic tools are allowing us to dissect the roles of genes and genetic architecture in social evolution, and eusocial insects are excellent models. Numerous hypotheses for molecular evolution of eusociality have been proposed, ranging from regulatory shifts in ‘old’ genes to rapid evolution of ‘new’ genes. A broad model to explain this major transition in evolution has been lacking. We provide a synthetic framework centered on the idea that different evolutionary processes dominate during different transitional stages, beginning with changes in gene regulation and culminating in novel genes later on. By considering multiple mechanisms as we ‘climb the social ladder’, we can test whether the transitions from solitary to simple sociality to complex sociality represent incremental changes or genetic revolutions.**

## Tracing the molecular basis of a major transition in evolution

The origin of eusociality, a rare but highly successful form of social behavior involving sterile workers and specialized reproductive castes, represents one of the major transitions in the evolution of life [1]. These evolutionary transitions are extremely important because once a new level of cooperation is attained (e.g., evolution of the first eukaryotes or origin of the first metazoans) many new ecological niches can be opened up and novel life histories can evolve. The transition from solitary living to eusociality shares the same hallmark consequences of the other major transitions – radical increases in functional complexity, the opening up of new major niches, and the development of a dominant role in widespread ecosystems [2,3].

Origins of eusociality are especially attractive for understanding major transitions because they provide experimentally tractable events [1,4]. Eusociality, which is defined by the presence of distinct reproductive and non-reproductive castes, has evolved many times, especially within the ants, bees, and wasps (Hymenoptera). Recently, there has been great interest in exploring social life in molecular terms [5], with numerous studies aimed at answering the question: ‘how does sociality evolve on a molecular level?’, with diverse taxa, techniques, and perspectives. Genomic studies of species with derived

eusocial behavior such as honey bees [6], paper wasps [7], and ants [8] are opening up many research horizons, but there is a severe paucity of data on the genomic mechanisms associated with the earliest transitions to eusociality. Some researchers have suggested that the transition to eusociality required few changes in DNA sequences, and was instead the result of shifts in the timing of gene expression [9], while others have argued that this transition could have entailed major changes at genomic and proteomic levels [10,11]. Despite enormous recent advances in both ecological and genomic studies [6–8], we still lack a broad model that is able to explain what happens at the molecular level during this major transition in evolution.

Such an understanding will be impossible if based on an oversimplified view that the evolution of eusociality describes a singular evolutionary transition. First, each eusocial lineage is unique, with distinct social traits and its own unique evolutionary history [12–18]. Second, we cannot overlook the important fact that many incremental steps are involved in the evolution of eusociality, including numerous pre-adaptations such as defensible nests and parental care [2,19–21]. In 1973, Evans and West-Eberhard [19] introduced the idea of a ‘social ladder’ to invoke stepwise transitions from solitary to eusocial in wasps, and were careful to clarify the analogy: ‘But of course each rung must have its own adaptive value [meaning that they are perfect strategies of their own], since many wasps inhabit each rung successfully and the evolution of sociality was by no means preordained.’

In considering the molecular evolution of eusociality, it is as crucial as ever to ‘climb the social ladder’ and consider different transitional stages, from the earliest origins of cooperative breeding through to the subsequent elaboration of colony-level traits in group-selected, highly eusocial units [22,23]. It is also essential that such comparisons be made within a well-grounded phylogenetic context. We begin by providing an overview of the different levels of sociality and transitions in eusocial evolution. We then briefly review current mechanistic hypotheses for the evolution of eusociality, focusing on their genomic context. Next we provide a framework for integrating these hypotheses into a phylogenetically-grounded synthetic conceptual model. Finally, we suggest appropriate taxa and set the stage for genomic studies that can be most informative in elucidating general principles about the molecular evolution of insect societies.

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**Levels of sociality and transitions in social evolution**

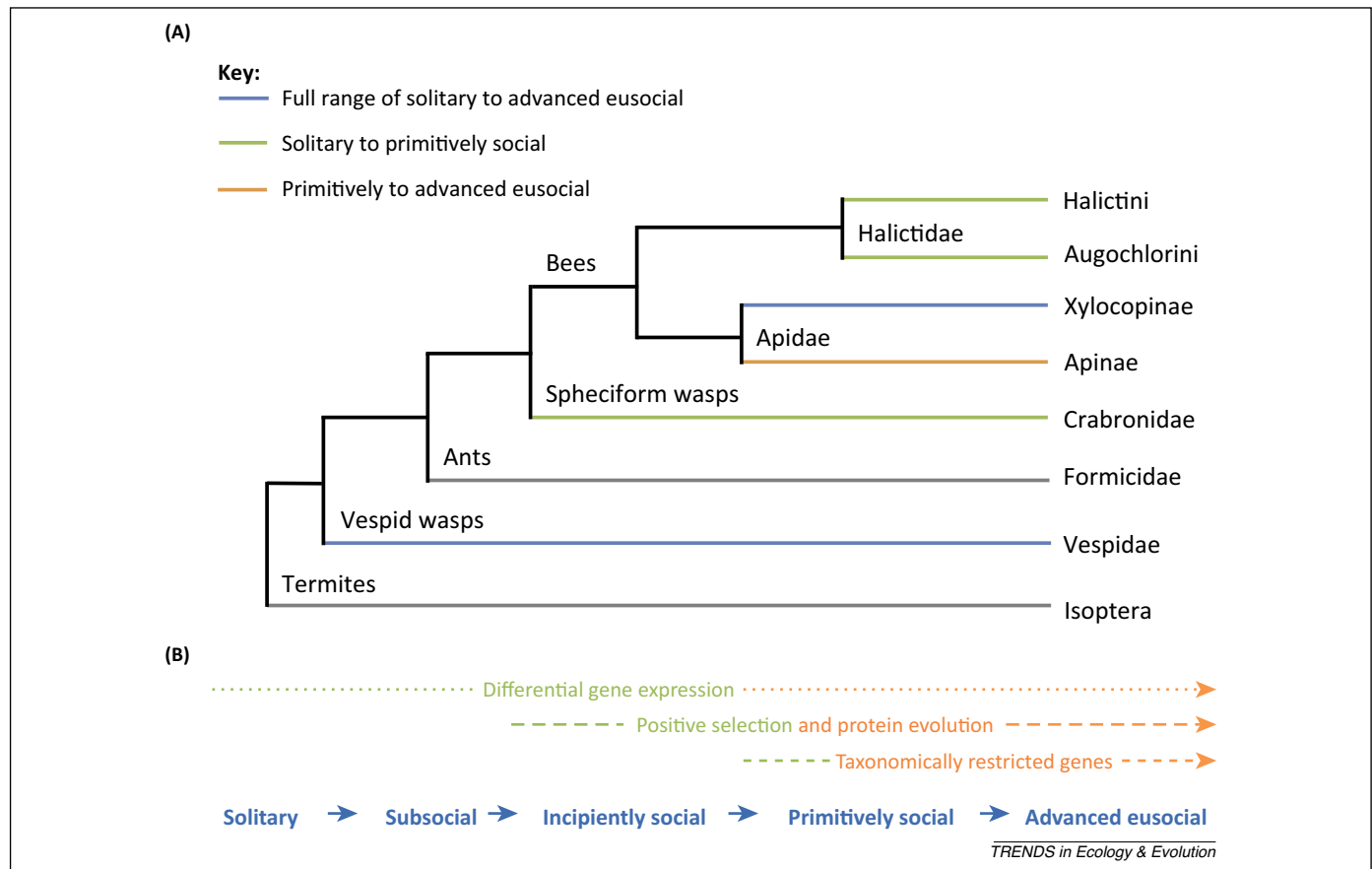
The social Hymenoptera (ants, bees, and wasps) are an especially informative group for studying social evolution because eusociality has evolved numerous times independently, and several lineages retain representative species at different levels of sociality (Figure 1A). It is generally agreed that leaps directly from solitary to eusocial are unlikely, and that intermediate stages are necessary during the evolution of eusociality [19,23–26]. Although there are various ways to view the different levels of sociality, and diverse terminology has been used in the past, here we define and focus on four distinct ‘rungs of the social ladder’, or levels of social complexity: subsocial, incipiently social, primitively social, and advanced eusocial (Table 1 clarifies which of the characteristics of eusociality are found at each level) [2]. ‘Subsocial’ refers to species with well-developed parental care; in Hymenoptera prolonged mother–offspring interaction is an essential preadaptation for the evolution of eusociality [2,21,26–28]. In Hymenoptera, incipiently social species are characterized by a rudimentary division of foraging and egg-laying tasks among individuals. All individuals are totipotent, retaining the ability to forage and reproduce, and can live solitarily. In ‘primitively social’ species, nests are initiated by founding maternal females, then transition into cooperative colonies upon the emergence of daughter workers [29]. Colonies are composed of two distinct castes: reproductive dominants

**Table 1. Levels of social complexity and behavioral traits associated with each social class<sup>a</sup>**

Social class	Cooperative brood care	Reproductive division of labor	Overlapping generations
Solitary	No	No	No
Subsocial	No	No	Sometimes
Incipiently social	Yes	Sometimes	Sometimes
Primitively social	Yes	Yes	Sometimes
Advanced eusocial	Yes	Yes	Yes

<sup>a</sup>Eusociality is defined by cooperative brood care, reproductive division of labor, and overlapping generations [2]. Solitary insects possess none of these characteristics, and subsocial, incipiently social, and primitively social insects exhibit one or more of these hallmarks. ‘Sometimes’ indicates that the trait varies within lineages or even within species within a lineage.

and foraging subordinates. Age- and body-size-based dominance hierarchies are common in these societies, all individuals retain the ability to mate, and caste-switching can occur. Advanced eusocial species are characterized by both morphologically distinct queen and worker castes, and complete reproductive division of labor in which females lose totipotency, queens monopolize reproduction, and workers are functionally sterile and forage for colony food provisions. Note that the above designations of level of sociality are wide generalizations that are intended to provide a context for thinking about evolutionary transitions by highlighting convergent features shared by many social lineages. However, there are also lineage-specific



**Figure 1. (A)** Overview of phylogeny of aculeate Hymenoptera (with the nonhymenopteran but eusocial termites as an outgroup), highlighting independent origins of sociality (colored branches), groups with species ranging from solitary to primitively social (green), primitively social to advanced eusocial (orange), solitary to advanced eusocial (blue), and all species advanced eusocial (grey). **(B)** The full range of the solitary to eusocial spectrum (blue) and predictions of which genomic mechanisms are hypothesized to operate at different transitional stages of social evolution (broken arrows).

characteristics for many social traits (Table 1). Solitary, intermediate, and social phenotypes differ in some important ways across lineages, and have followed different evolutionary trajectories, thus making it extremely important to consider these transitions for each independent origin of eusociality and within monophyletic groups of taxa.

Given the different levels of sociality found among extant species of eusocial insects such as Hymenoptera, it is useful to delineate how they represent different transitional stages in social evolution.

**Early stages: origins of sociality.** Individual solitary, maternal (subsocial) insects must complete all foraging and reproductive tasks to achieve lifetime reproductive success. Incipiently social insects evolved physiological switches to transition between reproductive and non-reproductive behavioral states [30]. It is thought that these transitions are achieved by changes in hormonal titers that are associated with changes in the expression of multiple sets of pleiotropically-linked genes [29,31].

**Later stages: elaboration of eusociality.** Transitions from primitively social to advanced eusocial societies involve obligate caste differentiation among females, and has been termed an evolutionary ‘point of no return’ [22], representing a major transition in evolution beyond which colony-level selection acts to produce novel social traits [32].

It is important to note that different mechanisms and selective forces can be involved during different stages of social evolution [31]. For example, it has been suggested that the origins of eusociality (defined by the first appearance of alloparental care in workers) might have more strongly depended on individual fitness and inclusive fitness benefits [23,30,33]. The elaboration of eusociality into highly derived forms (e.g., the existence of permanently sterile workers, or the presence of highly specialized morphological castes of workers in ants) appears to have been under strong colony-level selection for colony performance traits [22]. In light of possible differences in selective forces, as well as clear differences in the types of social

### Box 1. Additional genomic mechanisms in eusocial evolution

Importantly, there are additional genomic mechanisms which do not fall under one of the generalized major hypotheses presented in the main text, and that have been proposed to be associated with the evolution of social traits in insects. Studies on a derived social trait – the transition from one queen to multiple queens in fire ant colonies – suggest that major changes in colony social organization can be associated with the evolution of a Y-like ‘social chromosome’ with multiple linked genes related to social organization [72]. Recent studies on honey bees have highlighted the importance of epigenetic mechanisms, including DNA methylation, in caste differences [73]. DNA methylation might promote genomic flexibility and thus phenotypic plasticity [74], and could therefore play a role in the evolution of caste differences in eusocial insects [75,76]. Finally, high recombination rates (which are exceptionally high in some advanced eusocial species [77–80]) could also be linked to accelerated evolution of caste-related traits [81–83].

traits under selection at each transitional stage, we must also consider that different forms of molecular changes could underlie different stages in social evolution.

### Current hypotheses for the molecular evolution of insect societies

Currently, there are numerous mechanistic hypotheses related to the evolution of eusociality in insects. All address the question ‘how does eusociality evolve on a molecular level?’, but stem from different perspectives – including ethological, developmental, and molecular. Despite this proliferation of hypotheses, there has been little synthesis of different ideas across species and/or different stages in social evolution, even though many of these ideas are not mutually exclusive and might in fact be complementary and overlapping (Table 2). We provide here a very brief summary of some of the major hypotheses (others are summarized in Box 1). Some hypotheses focus more on the phenotypic level, and others more on the molecular level, but all of them involve elements addressable in a genomic context. To synthesize these ideas, we divide them into two major camps: those related to changes in gene expression, and those related to changes in genomic

**Table 2. Transitions in social complexity and empirical evidence for the genomic mechanisms hypothesized to operate at each stage of social evolution<sup>a</sup>**

Hypothesis	Subsocial to incipiently social	Incipiently to primitively social	Primitively to advanced eusocial
Ovarian ground-plan [29]	<i>Ceratina</i> [39] –	<i>Polistes</i> [41] +	<i>Apis</i> [34–36] +
Maternal heterochrony [27]	<i>Ceratina</i> [39] +	<i>Polistes</i> [41] +	<i>Bombus</i> [40] +
Genetic toolkit [44]		<i>Polistes</i> [46,48,52] + Bees [58] +	<i>Apis</i> [47,49,50] + Bees [58] + Ants [51] +
Novel genes [53]		<i>Polistes</i> [56] + <i>Polistes</i> [52] –	<i>Apis</i> [52–54,62] + Bees [63] + Ants [55,57] +
Protein evolution [58]			<i>Apis</i> [57,62] + Bees [59,63] + Ants [56,60] +
Conserved regulation [66]			<i>Apis</i> [61,66] + Bees [63] + Ants [60] +

<sup>a</sup>Note that for most standing hypotheses there is no empirical assessment for subsocial and incipiently social species. Importantly, most studies provide empirical data to assess and support a single hypothesis but are based on a single species. Few studies assess the relevance of alternative hypotheses and question their broad applicability across independent origins or levels of social complexity, nor compare species at different levels of sociality within a single monophyletic lineage. ‘+’ indicates support for a hypothesis from the cited study; ‘–’ indicates evidence against a hypothesis from the cited study.

sequence, noting that this artificial divide does not rule out the possibility of overlap between ideas.

#### *Gene expression-based hypotheses*

**The ovarian ground-plan hypothesis.** This was inspired by field observations of wasp behavior [29]. It posits that an uncoupling of solitary reproductive and foraging behaviors produced reproductive queen-like individuals and foraging worker-like individuals and, ultimately, eusocial queen and worker castes [29]. This idea predicts that gene networks related to reproductive and foraging behavior in solitary insects were coopted to regulate queen and worker behavior, respectively, during the transition from solitary to caste-containing societies. This hypothesis has received considerable attention, leading to the development of related ideas about the evolution of worker foraging division of labor [34]. Tests of this hypothesis using genetic data mainly come from advanced eusocial taxa [35,36], and some studies also challenge the general applicability of this hypothesis [37–39].

**The maternal heterochrony hypothesis.** Posits that reproductive division of labor evolved via a reorganization of the timing of offspring-care gene expression, not necessarily requiring the decoupling of foraging and reproductive regulatory pathways [27]. This idea predicts that maternal care and sibling care should be regulated by similar patterns of gene expression. Empirical evidence supporting this hypothesis comes from transcriptomic studies on advanced eusocial bumble bees [40], primitively social vespid wasps [41], and incipiently social small carpenter bees [39].

**The genetic toolkit hypothesis.** This hypothesis, driven by evo-devo considerations, proposes that regulatory changes in specific genes, pathways, or networks with conserved roles across species are important in the evolution of novel phenotypes [42,43]. An extension of this idea to social insects proposes that evolutionary changes in the regulation of small sets of deeply conserved genes with roles in solitary behavior (such as feeding, reproduction, and aggression) produced social traits such as social foraging and reproductive dominance [44,45]. Comparisons of advanced eusocial honey bees, ants, and primitively social paper wasps show some overlap in expression patterns of specific genes related to foraging [46,47], aggression [48,49], and caste differences [50,51], but a more recent analysis suggests a ‘loose toolkit’ based on key pathways rather than on specific genes [52]. The genetic toolkit idea is a more-general hypothesis than the ovarian ground plan and maternal heterochrony hypothesis, which can potentially encompass both the former hypotheses.

#### *Genomic sequence-based hypotheses*

**The novel genes hypothesis.** Proposes that eusociality, a novel social phenotype, is the product of the evolution of novel protein-coding genes. ‘Novel’ genes might have arisen from gene duplication followed by the neofunctionalization of duplicates, resulting in a rapid evolution of ‘taxonomically restricted genes’ that show no discernable sequence homology to previously described sequences. Evidence for this hypothesis comes from studies in advanced

eusocial honey bees, ants, and primitively social wasps where it was discovered that overexpressed genes in workers are more likely to lack homology to known sequences and to be taxonomically restricted to each lineage and/or Hymenoptera as a whole [53–57].

**The protein evolution hypothesis.** Proposes that the rapid evolution of specific genes or gene families led to changes in protein function that contributed to the evolution of social phenotypes. Previous studies examining the rates of protein sequence evolution across three lineages of solitary and eusocial bees uncovered evidence of positive selection on genes related to carbohydrate metabolism, glandular development, and signal transduction [58–60].

**The conserved regulation hypothesis.** This combines some elements of both DNA sequence-based and gene expression-based hypotheses. It proposes that changes in gene regulation prevail during the origins of insect sociality, and that changes in gene composition are more important during later stages and are related to lineage-specific social adaptations. A comparison of 12 insect genomes (including seven ants, one honey bee, and solitary flies and non-social wasps) revealed many changes in *cis*- and *trans*-regulatory elements between solitary and eusocial species, some of which are convergent across bees and ants [60]. In addition, each eusocial species contained thousands of novel genes, evidence of gene family expansions and rapid protein evolution, and these were suggested to be related to lineage-specific social adaptations [60].

### **A synthetic framework for studying the molecular evolution of eusociality**

In the following we highlight a framework for synthesizing some of the above hypotheses by addressing their potential roles at different transitional stages in social evolution (Figure 1B).

**Early stages: origins of sociality.** Hypotheses focusing on the earliest origins of sociality predict that transitions from solitary to incipiently social societies involve changes in the timing of gene expression, and all individuals remain totipotent into adulthood and throughout most of their lives, and are capable of performing reproductive and foraging tasks [27,31]. At the origin of sociality, such expression changes might start off as being environmentally-responsive, and stem from pre-existing developmental plasticity [31]. Based on this idea, our framework predicts that, early in social evolution, regulatory genomic changes, such as shifts in the timing and location of expression of conserved genes (akin to ovarian ground plan and maternal heterochrony hypotheses), are the primary drivers of social phenotypes. Then, in intermediate stages of social evolution from incipiently to primitively social roles become less flexible and more fixed (e.g., more stable caste differences). This would be associated with larger and more permanent caste-biases in expression and more fixed genomic changes, including both regulatory and protein coding sequence changes.

**Later stages: elaboration of eusociality.** Transitions from primitively to advanced eusocial societies are defined by the presence of distinct castes underlain by large differences in gene expression. Such caste-specific genes, which now only need to function in one caste rather than two castes, might be freed from pleiotropic constraints [11]. This could lead to stronger directional selection for changes in protein sequence related to elaboration of caste phenotypes, and this would be evidenced by signatures of positive selection in the genome, or even the birth of new genes associated with social traits [11]. Even at later stages of social evolution, once eusociality has reached ‘the point of no return’ [22], selection acts strongly at the level of the colony – and this could pave the way for more dramatic changes in the structure of gene networks, rapid protein evolution, gene duplication, and the rise of taxonomically restricted genes to facilitate the evolution of novel colony-level traits [11]. Recent studies have sought to discover how novel genes become integrated into existing developmental gene regulatory networks [61,62].

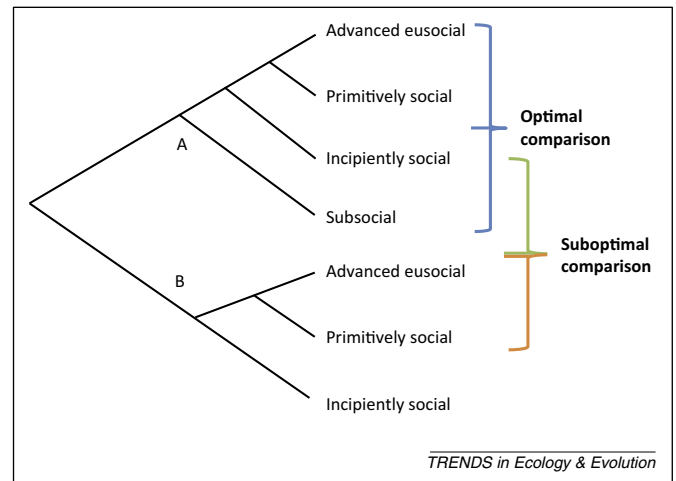
Elements of the above framework have been advocated by other authors in conceptual models [9,31,60], and although the framework is hypothetical it is directly testable. Additional studies are needed to identify which genes vary in their expression according to social roles, and how genomic sequences have evolved across a social spectrum. It is certainly possible that multiple mechanisms operate simultaneously at different stages of social evolution. However, we need a more complete assessment of the relative contributions of each type of genomic change listed above, and to consider which changes operate at different transitional stages of social evolution. Work of this type would allow unprecedented synthesis of genetic and genomic hypotheses for the evolution of sociality into a broad new framework.

To put the ideas presented in this framework to the test, phylogenetically conserved comparisons across the full range of solitary to eusocial species will be necessary to determine the relative roles of taxonomically restricted genes relative to positive selection on standing genetic diversity (coding or regulatory) as mechanisms for the evolution of social complexity within well-resolved monophyletic groups (Figure 2). General principles can potentially then be extrapolated by comparing the types of genomic changes that occur between different lineages (Table 2). A very recent study [63] illustrates that the field is already moving in this direction. By comparing the whole genomes of 10 select species of bees from multiple, independently evolved social lineages, this study revealed increases in both the complexity of gene regulation and more-pronounced changes in gene complement in more highly-social species [63]. These results agree with the predictions of our framework; however, future studies that include species representing the full range of solitary to advanced eusocial species within lineages will still be necessary to provide more definitive tests of the predictions of our framework.

### A way forward: the most informative taxa and genomic studies

#### The most informative taxa

Studies on genomics of sociality in honey bees and ants have been ground-breaking in both developing new ideas



**Figure 2.** A phylogenetic representation for suggested contrasts in studies comparing social lineages with different levels of social complexity. Node (A) represents one independent origin of sociality, and (B) represents a separate independent origin of sociality. The optimal comparison among levels of social complexity is within an independent origin of sociality (and also within a monophyletic lineage). In the suboptimal comparison all represented social levels are compared, but include two different origins of sociality (A and B); again the within-lineage comparison is superior to the across-lineage comparison because it controls for many other differences between independent origins of sociality.

about genomic mechanisms underlying social evolution and studying the evolution of derived social traits [4,8,64,65]. In addition, work on these more common models paved the way with respect to genomic technologies and analytical methods [60,66–68]. However, studies of advanced eusocial species alone cannot provide the wealth of social transitions and the full range of social levels provided by a comparative perspective including some less-studied taxa, such as bees in the family Halictidae, bees in the subfamily Xylocopinae, and the wasp family Vespidae (Figures 1A and 2). We suggest that a focus on studying genomic changes within these monophyletic groups will provide more-complete, and thus more-informative, insights into the genomics of social transitions. In addition, data from each lineage can then be compared to other lineages to determine whether similar types of genomic changes indicate a common architectural basis to sociality (Table 2) [52].

**Halictidae.** Within this bee family there are two independent origins of sociality: once in the tribe Augochlorini and once in the tribe Halictini [12]. Species range from solitary to primitively social, but there are no advanced eusocial species. Primitive sociality has been lost up to 12 times in this lineage, providing numerous comparisons for solitary to primitively social behavior [13].

**Apidae.** Species within this bee family range from solitary to advanced eusocial, with two independent origins of advanced eusociality, once in the subfamily Xylocopinae and once in the subfamily Apinae. In the Xylocopinae, sociality has been lost at least four times [14]. Advanced eusociality has evolved at least once in the allodapine bees. In the Apinae, species range from primitively social to advanced eusocial. There is one loss of sociality in the orchid bees [15]. The bumble bees are commonly regarded as being primitively social despite many advanced eusocial

traits – namely queen pheromones, swarm founding, and thermoregulation [16]. Advanced eusociality is exhibited in the stingless and honey bees.

*Vespidae*. Members of the *Vespidae* show the full range of behavior, from solitary to advanced eusocial. It is currently unresolved whether there is one or two independent origins of sociality within this family of wasps. Under the single-origin scenario [17], all the transitional stages are represented within a single, monophyletic lineage. Under the dual-origin scenario [18], incipient sociality evolved in the *Stenogastrinae* independently of the *Polistinae*.

#### Genomic studies

A major strength of our framework is the introduction of a guiding hypothesis that is directly testable using empirical studies. These tests will require genome-scale studies of the aforementioned groups – less-studied, but highly-informative taxa – which have lagged behind other social insects but are beginning to come to fruition for individual species within each lineage (*Halictidae* [69]; *Xylocopinae* [39]; *Vespidae* [52,56]). The next important step will be coordinated, multi-species sequencing and comparative genomic analyses. Below, we outline specific predictions made by our framework and suggestions for testing them using genomic data.

**Prediction 1.** Evolutionary changes in gene regulation (e.g., ovarian ground-plan and maternal heterochrony hypotheses) will prevail at very early stages of social evolution (subsocial to incipiently social), as well as later stages of social evolution. This can be tested using transcriptomic studies of gene expression patterns related to maternal behavior, queen–worker caste differences, and worker behavioral specializations across multiple species at different stages in social evolution.

**Prediction 2.** Conserved genomic toolkits are central to the molecular evolution of sociality, and these are shared across lineages and across all stages of social evolution. By sequencing genomes and transcriptomes across the full social spectrum (subsocial to advanced eusocial) we can identify recurrent sets of genes, pathways, and *cis*-regulatory elements, especially transcription factors, that are common to shared social traits (such as queen–worker castes, social foraging, and aggression) at each stage and independent origin of sociality.

**Prediction 3.** There are more abundant and pronounced changes in protein-coding sequences in genes related to social phenotypes during the mid and late stages of social evolution (incipiently social to primitively social to advanced eusocial) compared to early stages. Sequencing of multiple, whole genomes within monophyletic groups for select species representing transitional stages in social evolution can provide information on expansions or contractions in gene families, rates of protein sequence evolution, or evidence of selection on protein or regulatory sequences.

**Prediction 4.** Although novel genes are present in all species, there will be an increasing role for novel genes

#### Box 2. Outstanding questions

- Which genomic mechanisms are operating at the origin of eusociality, and which during elaboration? Are they the same or different?
- Is genomic evolution of eusociality repeatable? In other words, are similar types of genomic changes during similar evolutionary transitions in independent lineages the same or different?
- Are there general principles that can be applied to social evolution in non-Hymenoptera, such as termites, naked mole rats, and even humans?

in social phenotypes in later stages of social evolution (primitively social to advanced eusocial) compared to early and mid-stages. With whole genomes of multiple species at each stage of social evolution we can identify species- and lineage-specific taxonomically restricted genes. Their putative functions or roles in social phenotypes can be further addressed through integrating transcriptomic data, with the prediction that novel genes will be more often differentially expressed in association with social traits in advanced eusocial species (e.g., caste differences) compared to social traits found in incipiently social species (e.g., maternal care, reproductive asymmetries between individuals).

In the long term, as more studies accumulate, synthesis of genomic data across social transitions, and across multiple monophyletic lineages, can inform on the extent to which different molecular evolutionary changes are involved at different stages of social evolution. Importantly, the ‘social ladder’ framework is only one of many possible explanations for the molecular evolution of eusociality, and can be falsified if data are not in line with the predictions suggested above. It is certainly conceivable that other explanations might prevail, such as an equally important role for novel genes throughout the different stages of social evolution. For example, novel genes are well known to be found throughout the tree of life [70], and have been proposed to be important for the evolution of novel traits not related to sociality [71].

#### Concluding remarks

Understanding the genetic underpinnings of social behavior and how behavior evolves at a genetic level is a central issue in the evolutionary development of social complexity. While important first steps have been taken using highly eusocial species, we propose that future research should focus on the early stages of sociality. These data will provide insights that will help to inform earlier studies by identifying the types of genomic changes associated with both early and late-stage social evolution. We suggest that the types of genomic mechanisms at each stage will likely differ due to differences in the level of selection and the types of social traits being considered. A broader phylogenetically grounded comparative approach could allow an unprecedented synthesis of genetic and genomic hypotheses for the evolution of sociality into a broad new framework. The resulting benefits could extend widely into the evo-devo paradigm. Outstanding questions are listed in [Box 2](#).

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