

Functional Heterogeneity in Superorganisms: Emerging Trends and Concepts

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Abstract

Social insects are biological benchmarks of self-organization and decentralized control. Their integrated yet accessible nature makes them ideal models for the investigation of complex social network interactions, and the mechanisms that shape emergent group capabilities. Increasingly, interindividual heterogeneity, and the functional role that it may play, is seen as an important facet of colonies’ social architecture. Insect superorganisms present powerful model systems for the elucidation of conserved trends in biology, through the strong and consistent analogies that they display with multicellular organisms. As such, research relating to the benefits and constraints of heterogeneity in behavior, morphology, phenotypic plasticity, and colony genotype provides insight into the underpinnings of emergent collective phenomena, with rich potential for future exploration. Here, we review recent advances and trends in the understanding of functional heterogeneity within social insects. We highlight the scope for fundamental advances in biological knowledge, and the opportunity for emerging concepts to be verified and expanded upon, with the aid of bioinspired engineering in swarm robotics, and computational task allocation.

Key words: biological heterogeneity, model system, superorganism, collective behavior, phenotypic plasticity

The emergence of complex collective societies from formerly solitary organisms constitutes one of the most significant evolutionary shifts in the history of life (Wheeler 1926, Hölldobler and Wilson 1990, Field et al. 2010, Helanterä 2016). This transition is notable for its expansion of biological organization to the level of the ‘superorganism’ (Wheeler 1911), with concordant implications for selective processes, and the myriad emergent (Lewes 1875) phenomena that supervene as a result (Wheeler 1928, Bonabeau et al. 1997, Gardiner and Grafen 2009, Hölldobler and Wilson 2009, Cremer et al. 2018). Importantly, like their analogs at lower organizational levels, such as cells within multicellular organisms, or tissue types within an organ system, invertebrate societies possess intragroup heterogeneity that can be characterized as functional, that is, contributing to their fitness (Wilson 1968, Anderson and McShea 2001, Hart and Ratnieks 2001, Oldroyd and Fewell 2007, O’Shea-Wheller et al. 2017). Such heterogeneity may be manifest in genotype (Jones et al. 2004, Oldroyd and Fewell 2007), phenotype (Robinson et al. 2008b, 2011), task allocation (Seeley and Kolmes 1991, Sendova-Franks and Franks 1993, Gordon 1996), or indeed, emerge from latent environmental stimuli, without the need for interindividual differences between workers (Deneubourg and Franks 1995, Gordon

and Mehdiabadi 1999, Theraulaz et al. 2003). In contrast to single organisms, however, insect colonies may be readily deconstructed, manipulated, and experimentally altered, from the level of the society, down to that of the individual (Johnson and Linksvayer 2010, Kennedy et al. 2017). As such, these systems can provide an accessible entry point for empirical research, affording valuable insights into the significance of biological heterogeneity across organizational levels, and spatial scales (Breed et al. 2002, Strassmann et al. 2002, Kennedy et al. 2017).

The important influence of *variation* among individuals, aside from the typical or average traits within a group, has been acknowledged as a key avenue of investigation throughout the history of biological and complex systems research (Thomson 1917, Buss 1983a, Van Baalen and Beekman 2006, Burns and Dyer 2008, Clobert et al. 2009, Youn and Gabrilovich 2010, Dall et al. 2012). Indeed, from the origins of multicellularity (Hanson 1958, Buss 1987), to fundamental evolutionary processes at a community scale (Clobert et al. 2009), diversity of form and function exists not only as random ‘noise’, but as a functional property of biological systems, intertwined with selective pressures (Thomson 1917, Buss 1983b, Kennedy et al. 2017, Jolles et al. 2020). Such

heterogeneity appears to emerge almost ubiquitously in nature, spanning systems as taxonomically disparate as quorum sensing in bacteria, where population-level variability enhances biofilm formation (Anetzberger et al. 2009, Grote et al. 2015); spatial cohesion in bird murmurations, in which heterospecific avoidance defines flock structure (Jolles et al. 2013), and a diversity of complex behaviors in social insects, as expanded upon here (Weidenmüller 2004, Oldroyd and Fewell 2007, Masuda et al. 2015, Saffre et al. 2018; Fig. 1). This would seem to indicate that it is of functional importance in the adaptation of biological collectives to their environment.

Social insects display key traits that predispose them to complex forms of functional heterogeneity, while at the same time, providing excellent models from which to transfer these concepts to other systems. Specifically, the limits of cognitive capacity at the individual level (Bonabeau et al. 1997, Leadbeater and Chittka 2007), coupled with the advantages of substantial complexity at the group level (Theraulaz et al. 1998a, Kang and Theraulaz 2016), necessitate particularly effective forms of colony self-organization (Fewell 2003, Duarte et al. 2011, Mlot et al. 2011, Saffre et al. 2018, Strömbom and Dussutour 2018). This seemingly paradoxical interaction leads to emergent properties—collective attributes that are greater than the sum of their constituent parts (Lewes 1875, Goldstein 1999, De Wolf and Holvoet 2005)—that often rely on individual variation (Weidenmüller 2004, Burns and Dyer 2008, Pinter-Wollman 2012, O’Shea-wheller et al. 2017, Saffre et al. 2018). Consequently, insect colonies exhibit conserved interaction network attributes,

common to a myriad of other complex systems in biology, yet provide a pre-eminent opportunity for their study in the context of multilevel selection (Camazine et al. 2003, Fewell 2003, Naug 2008, Charbonneau et al. 2013, Guo and Wilensky 2016, Gernat et al. 2018).

Many inquiries into the adaptive benefits of heterogeneity in insect colonies have been made, and both the theories, and methodologies employed, have evolved over time. Early works focused on the concepts of ‘division of labor’ (Smith 1776, Buckingham 1911), and caste polymorphism (Gregg 1942, Wilson 1968), especially in ants. Such striking examples of behavioral and morphological heterogeneity in workers, though confined to a small minority of genera (Powell and Franks 2006), provided a rich substrate for the examination of functional variation. A central tenet of these investigations, was the idea that, as in our own species (Smith 1776), the specialization of workers for specific task groups improved efficiency, and thus overall colony productivity (Wilson 1968). Consequently, the questions of appropriate (behavioral) caste ratio, task flexibility, and their interactions with ecological pressures (Richards and Richards 1951, Wilson 1968) were paramount in early research. Furthermore, the mechanisms of caste determination were recognized as vital to understanding how such heterogeneity was regulated, and hence, how ‘optimal’ interindividual variation might arise (Wheeler 1986, Hölldobler and Wilson 1990). This question continues to be explored, with multiple influences now recognized as converging to shape caste determination, from the interaction between

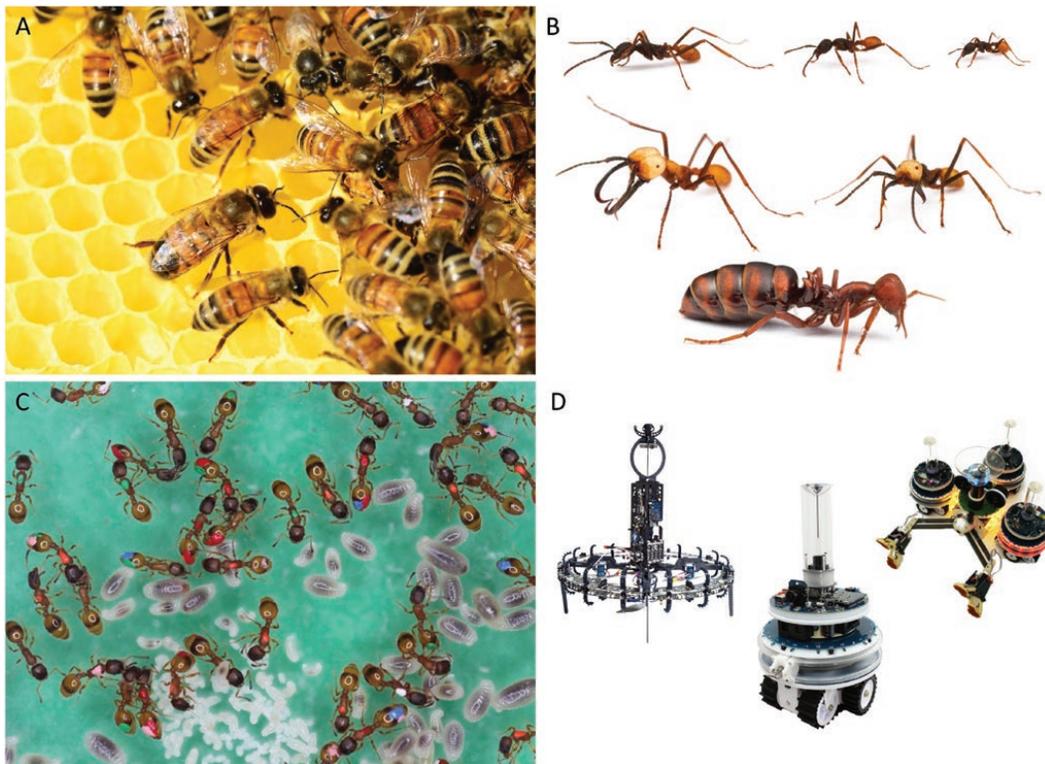


Fig. 1. Manifestations of functional heterogeneity. (A) *Apis mellifera* has monomorphic workers, but behavioral diversity emerges through genotypic, epigenetic, and experiential mechanisms. (B) *Eciton burchellii* demonstrates striking caste polymorphism via epigenetic regulation. Distinct divisions exist between minor and media workers (top), submajors (middle right), majors (middle left), and queens (bottom) (Franks et al. 2001). Photographs courtesy of Daniel Kronauer. (C) *Temnothorax albipennis* workers show variability in their nest assessment behavior, as a consequence of heterogeneously distributed acceptance thresholds. Workers are monomorphic, but paint marks reveal differences. Photograph courtesy of Nigel Franks. (D) ‘Swarmanoid’ robots utilize heterogeneous swarms of ‘eye-’, ‘hand-’, and ‘foot-bots’, to complete tasks. Photographs courtesy of the Swarmanoid project.

environment and epigenetics (Wheeler 1986, Hölldobler and Wilson 1990, Fjerdingstad and Crozier 2006), to the role of patrilineal genotype (Hughes et al. 2003, Hughes and Boomsma 2008, Schwander et al. 2010). Interestingly, there is a growing body of research to indicate that many of the genetic pathways regulating polyphenism are conserved across eusocial insect taxa, despite the independent origins of their sociality (Corona et al. 2016).

Functional variation in the social insects is far from limited to fixed notions of caste and morphology, however (Gordon 2016; Fig 1). Indeed, it exists in systems where these distinctions are hard, if not impossible, to make, and does not occur in a social vacuum, absent environmental feedback (Sendova-Franks and Franks 1993, Breed et al. 2002, Robinson et al. 2009). Accordingly, an extensive body of research examines heterogeneity and task allocation in species with monomorphic workers. This addresses both the cues that influence task propensity, and the genetic, physiological, and environmental feedback mechanisms that underlie phenotypic plasticity (Johnson and Linksvayer 2010, Jeanson and Weidenmüller 2014, Yan et al. 2014, Jeanne 2019). When characterizing such systems, the term 'flexible heterogeneity' is salient, as there appears to be a general trend of increased behavioral totipotency within less socially derived taxa (Bourke 1999, Anderson and McShea 2001, Boomsma and Gawne 2018, Jeanson 2019). Consequently, in many species, the attributes that vary between individuals are not necessarily fixed, allowing workers to alter their behavioral repertoires to better meet the needs of the colony. Notwithstanding this flexibility however, certain factors are known to underpin a baseline heterogeneity in behavioral propensities. Important factors include the influences of genotype (Page et al. 1995, Julian and Fewell 2004, Oldroyd and Fewell 2007, Dolezal and Toth 2014), age (Seeley and Kolmes 1991, Yang et al. 2009, Mersch et al. 2013), nutritional state (Toth and Robinson 2005, Charbonneau et al. 2017), experience (Ravary et al. 2007, Leadbeater and Dawson 2017), and crucially, task demand and social information (Sendova-Franks and Franks 1995, Robinson et al. 2008a, Couzin 2009, Pinter-Wollman et al. 2013, Pagliara et al. 2018).

Engendered by flexible heterogeneity, the qualities of interchangeability and redundancy emerge as relevant features of many social insect systems (Anderson and McShea 2001). If workers are effectively totipotent in behavior, this confers clear advantages to the colony in terms of robustness and flexibility, as there is no need to replenish specialized individuals with like-for-like replacements. Instead, any worker can fill a role as task demand requires, in a self-organized fashion (Robinson et al. 2009). Such versatility appears in stark contrast to the concept of division of labor by morphological specialization, permitting rapid responses to environmental change. Furthermore, functional variation may arise from heterogeneity in the environment itself, rather than from intrinsic differences between workers, thus producing collective behaviors that are powerfully adaptive at the colony level, despite being fundamentally simple from the perspective of individual heuristics (Bonabeau et al. 1998, Greene and Gordon 2007, Fujioka et al. 2017).

The adaptive significance of heterogeneous individual attribute distributions has been identified in a diversity of systems. Examples encompass colony homeostasis (Jones et al. 2004, Weidenmüller 2004), social immunity (Baer and Schmid-Hempel 2003, Tarry 2003, Hughes and Boomsma 2006, Cremer et al. 2018), the regulation of foraging (Spaethe et al. 2007), and collective decision-making (Robinson et al. 2011, O'Shea-wheller et al. 2017). One notable manifestation of the latter is in heterogeneously distributed response thresholds, which solve specific behavioral challenges, by utilizing diversity in perceptions (Jones et al. 2004, Weidenmüller

2004, Spaethe et al. 2007, Robinson et al. 2011, O'Shea-wheller et al. 2017). Such phenomena are of particular interest, due to their potential for generating emergent collective behaviors that are decentralized (Camazine et al. 2003, Ravary et al. 2007), robust to network perturbations (Dorigo et al. 2000, Robinson et al. 2009), and rapidly adaptive in response to changing environments (Theraulaz et al. 1998b, Anetzberger et al. 2009, Duarte et al. 2011).

As experimental tools and methodologies improve, opportunities arise to manipulate threshold distributions in well-studied systems, and thus determine the specific characteristics of adaptive heterogeneity in life history scenarios. Some studies have, to date, been able to do this, although only in the context of eliminating variation completely (Jones et al. 2004), and fundamentally altering social conditions (Breed et al. 2002, Cook and Breed 2013). Such manipulations necessarily disrupt the underlying threshold structure, and as a corollary, likely generate compensatory shifts, as the system adjusts to these changes (Theraulaz et al. 1998b). Despite the challenge of potentially confounding adjustments, however, work in bacteria has shown that artificially generated threshold heterogeneity fails to match the performance of that in natural populations (Anetzberger et al. 2009). Considerably more complex manipulations could feasibly be applied to social insect colonies, with intriguing implications. As such, the research trajectory of functional heterogeneity shows a broadening of scope, from initial studies of discretely categorized and fixed variation, to investigations of flexible task allocation, and the fundamental properties of heterogeneous distributions themselves. This serves to highlight the importance of functional heterogeneity as a recurring concept, underlying much of the complex and emergent behavior observed in social insect societies.

In the following sections, we review three key aspects in the understanding of functional heterogeneity within social insects. This includes identification of emerging trends, and the future research questions that such systems are helping to elucidate. Because our focus is on *functional* heterogeneity, we also highlight the relevance of this research to the fields of applied science and engineering, and its use in the practical verification and exploitation of emerging principles. We aim to selectively emphasize pertinent areas of investigation with strong potential for future advancement. We conclude by underlining their broader value for addressing fundamental questions in biology and network science.

Genes and Functional Heterogeneity

In order to understand the benefits, costs, regulation, and maintenance of adaptive variability within insect societies, the roles of the genome, epigenome, and transcriptome, must all be taken into account (Robinson et al. 2008a, Schwander et al. 2010, Toth et al. 2010, Colgan et al. 2011). Insect colonies share conserved genetic characteristics, and display high levels of relatedness, ostensibly due to physiological differentiation into germ and soma castes, and overlapping generations of sterile workers (Boomsma and Gawne 2018). Despite this, however, a colony is able to produce diverse variation in the form and function of its constituent members, through both epigenetic regulation (Yan et al. 2014), and heterogeneity between individual genotypes (Oldroyd and Fewell 2007). When discussing genotypic variation, it is paramount that such processes are not seen in isolation, but rather, in the context of the individuals' environment. This is well-exemplified in the case of social behavior. Genes do not directly 'code' individual behavior, instead, they provide a substrate through which the influences of environment and social information interact, and it is the resultant

combination of these influences that manifests as behavioral phenotype (Robinson 2004). Additionally, environment may alter genotype itself over an evolutionary timescale, principally via natural selection for favorable phenotypes (Robinson et al. 2008a). As such, the influence of genotype on heterogeneity within insect colonies is an inherently bi-directional, nonlinear feedback process between genes and the environment, operating over several temporal and organizational scales (Oldroyd and Thompson 2006, Robinson et al. 2008a, Yan et al. 2014).

The question of how genotypic variation shapes polyphenism in social insects is an extensively studied one, and evidence exists of its contribution to functional heterogeneity in task allocation (Page Jr. 1991, Waddington et al. 2010), worker polymorphism (Julian and Fewell 2004), and colony homeostasis (Jones et al. 2004, Weidenmüller 2004). Interindividual variation in genotypes within colonies can arise from several sources. These include multiple queen matings, or polyandry, leading to coincident patriline, as seen in the honey bee *Apis mellifera* (Linnaeus 1758) (Hymenoptera: Apidae) (Page 1980; Fig. 1A), the presence of multiple queens in a colony, or polygyny, as exemplified by the leafcutter ant, *Acromyrmex versicolor* (Pergande 1893) (Hymenoptera: Formicidae) (Julian and Fewell 2004), and meiotic recombination, a process that occurs at significantly higher frequencies within the social hymenoptera (Wilfert et al. 2007, Kent et al. 2012). Notably, polyandry, and polygyny, generate separate ‘subfamilies’ within a colony (Oldroyd and Fewell 2007), displaying genotypes that differ to a greater degree than might be predicted by classical kin selection theory (Hamilton 1964). While such diversity necessarily imparts costs by reducing worker relatedness (Page et al. 1989), it may also alter behavioral propensities between worker groups, resulting in the emergence of functionally heterogeneous collective behaviors. Early investigations in *A. mellifera* challenged the notion that task propensity was entirely the result of environmental effects, by demonstrating that patriline did indeed influence task propensity, and thus allocation, in workers (Frumhoff and Baker 1988, Page et al. 1989). Furthermore, the specific combination of patrilines—and thus worker subgroups—present in colonies of this species, has been shown to effect key life-history parameters (Oldroyd et al. 1992; Fig. 1A).

The influence of genetic recombination upon functional heterogeneity is less clear. Putative mechanisms by which this process may influence the evolution of heterogeneous worker behavior have been proposed in *A. mellifera*, with some evidence for higher rates of recombination in genomic regions containing behavioral genes (Kent et al. 2012). However, additional analyses have contested such a link (Hunt et al. 2013), and indeed, a more recent study found no strong association between recombination and gene expression patterns (Wallberg et al. 2015). As such, the potential role of recombination remains interesting, but requires further examination. While the potential benefits of genetic diversity have been highlighted thus far, it should also be emphasized that, though often functional, genotypic variation may not always be collectively advantageous. Notably, genotype has been found to bias reproductive differentiation in some species, both through nepotistic rearing (Page et al. 1989), and direct developmental mechanisms (Hughes and Boomsma 2008), thus constituting an example of ‘selfish’ functional heterogeneity, that is advantageous at the genotypic, but not at the colony, level.

Much of the genotypic influence on collective behavior, and task-allocation, is postulated to act through worker response thresholds to various stimuli, generating self-organized processes (Jeanson and Weidenmüller 2014). An excellent empirical example of this can be observed in the thermoregulatory behavior of two species of bee, *A. mellifera*, and *Apis florea* (Fabricius 1787) (Hymenoptera:

Apidae), in which genotypic variation between workers enables robust thermoregulation (Jones et al. 2004, 2007). Specifically, genetically determined fanning threshold variation ensures a graded response to deviations from homeostatic equilibrium, thus avoiding overcompensation, and providing superior control when compared with homogenous models. Interestingly, this system is mirrored in the bumble bee *Bombus terrestris* (Linnaeus 1758) (Hymenoptera: Apidae), for which multiple matings are rare, suggesting convergent forms of functional heterogeneity, via different mechanisms (Weidenmüller 2004). Such processes appear to be highly derived, and serve as testament to the ability of genotypic variation to produce emergent phenomena through biological heterogeneity. Genotypic variation alone, however, is very much the ‘tip of the iceberg’, when it comes to interindividual variation in social insect colonies. Principally, this is because it has the special requirement of either multiple lineages, or genetic recombination. As such, for a more complete understanding of how genes influence functional heterogeneity, the complex interaction between epigenetics and the transcriptome must be considered.

Unlike genotypic variation, epigenetic and transcriptomic heterogeneity can arise purely as a result of an individual’s existing genotype interacting with its environment (Yan et al. 2014, 2015; Corona et al. 2016). Gene expression varies in response to environmental stimuli, and crucially, persists after cell division, potentiating variation between individuals over both a short, and long, timescale (Yan et al. 2015). Notably, this process has been implicated in worker polymorphism (Chittka et al. 2012, Matsuura et al. 2018), temporal polyethism (Yan et al. 2014), behavioral plasticity (Sumner et al. 2006, Ingram et al. 2011, Yan et al. 2015, Simola et al. 2016), and numerous other forms of heterogeneity across a plethora of species (Glastad et al. 2015). Current research is revealing the complexity of how genes and the environment interact to transcribe products that effect behavior, and in turn, how social behavior itself feeds back into, and influences, the process (Yan et al. 2014). While there is an extensive back-catalog of literature relating to epigenetics in social insects, the roles of specific molecular processes, such as DNA methylation, and microRNA modulation, are particularly relevant to behavioral plasticity and task regulation (Patalano et al. 2012, Yan et al. 2015, Corona et al. 2016). Notably, however, studies in both ants and wasps have found contrasting evidence of the importance of these processes (Patalano et al. 2015, Libbrecht et al. 2016, Standage et al. 2016), and thus the elucidation of epigenetic mechanisms warrants rigorous ongoing investigation.

Epigenetic regulation constitutes an important driver of functional heterogeneity that is both self-organized, and labile (Yan et al. 2014). This is well demonstrated by the ant *Harpegnathos saltator* (Jerdon 1851) (Hymenoptera: Formicidae), in which phenotypic plasticity for the task of reproduction, and its concomitant behavioral repertoire, is an epigenetically regulated process (Bonasio et al. 2010). Specifically, workers of this species may ascend to the role of queen, or gamergate, when the existing reproductive queen is lost (Liebig et al. 1998, Penick et al. 2011). Furthermore, gamergates removed from the colony, and kept in isolation, can revert back to the status of worker, both behaviorally, and physiologically, thus ensuring that the reproductive demands of the colony are met, in a self-organized fashion (Yan et al. 2014). This constitutes, arguably, one of the most striking examples of flexible heterogeneity in ants, for which reproductive differentiation is often permanent (Chittka et al. 2012). While the exact mechanisms underpinning the transition are not yet known, research has shown that genes involved in longevity and neuroendocrine function are differentially expressed between workers and gamergates of *H. saltator*, demonstrating the ability of epigenetics to simultaneously alter both

neurology and physiology (Bonasio et al. 2010, Simola et al. 2013, Yan et al. 2014). As such, epigenetic processes represent a powerful, but flexible, toolkit, able to shape variation in both form and function in order to meet the adaptive needs of the colony, yet requiring only a single genome, shared among individuals.

While significant advances have been made in the understanding of how genes influence biological heterogeneity in social insects, the vast temporal, and hierarchical, complexity inherent to these processes affords ample room for further inquiry. Three promising avenues of research are outlined as follows. First, many systems exist in which the benefits of genotypic variation, as a consequence of multiple lineages within colonies, are not clear, despite the potential relatedness costs (Jeanson and Weidenmüller 2014). Interestingly, increased genotypic diversity correlates with a concordant increase in social complexity within certain taxa (Yan et al. 2014), and thus the evaluation of such systems has the potential to uncover novel forms of functional heterogeneity. Second, further research examining the heritability of epigenetically regulated functional heterogeneity will be needed, as studies indicate that the process occurs (Gordon 2013, Linksvayer 2015); however, the exact mechanisms are not yet well-defined. Additionally, intergenerational epigenetic inheritance itself represents a complex challenge in eusocial insects, as reproductive differentiation can effectively decouple epigenetic effects in workers from direct transmission (Glastad et al. 2015). Finally, the question of how epigenetic mechanisms generate persistent phenotypic variation, that is simultaneously plastic, requires further elucidation (Patalano et al. 2015, Corona et al. 2016), especially in relation to the specific molecular processes underpinning individual responses to the environment.

Phenotypic Plasticity and Its Role in Functional Heterogeneity

Phenotypic plasticity is a fundamental driver of trait diversity in groups, and thus plays a significant role in the emergence and maintenance of functional heterogeneity. Phenotypic plasticity refers to some of the changes in an organism's morphology, physiology, and behavior that occur in response to a unique environment. This can result from the alteration of developmental events, or via the ability of an organism to alter its phenotype in response to changing environmental conditions (Kelly et al. 2011). One can conceptualize phenotypic plasticity as mapping environmental gradients to trait expression, via a developmental reaction norm (DRN) curve (Schlichting and Pigliucci 1998). This concept encompasses the processes that alter phenotype throughout the ontogenetic trajectory; conveys the fact that different aspects of the phenotype are correlated; and represents a genotype's ability to produce different phenotypes in different environments. The capacity of organisms to deal with different environmental contingencies, as described by a DRN, is shaped by evolutionary forces: plasticity varies in amount, pattern, rapidity, and reversibility (Schlichting and Pigliucci 1998). Adjustments can range from fixed, irreversible developmental trajectories, to rapid and reversible changes (Kelly et al. 2011). As such, phenotypic plasticity can be construed very broadly, to include learned behaviors, as these are still a result of interactions between the genotype and environment (DeWitt and Scheiner 2004). Social insects can display extreme forms of phenotypic plasticity (Kennedy et al. 2017), and this may play an important role in their ecological success (Manfredini et al. 2019). Here, we consider plasticity in morphology and behavior as two particularly notable forms of plasticity in superorganisms.

The most conspicuous examples of functional plasticity in insect superorganisms are those of reproductive and morphological caste differentiation. Reproductive caste determination varies among

social insect species, in the respective influences of genotype and environment (Smith et al. 2008, Schwander et al. 2010). Indeed, the role of both is important in shaping functional morphological heterogeneity, as observed in the worker castes of termites, and some ants. In both new world army ants of the genus *Eciton* (Latreille 1804) (Hymenoptera: Formicidae), and *Acromyrmex* (Mayr 1865) (Hymenoptera: Formicidae) leafcutter ants, there is an interplay between genetic and environmental influences in determining worker caste diversity (Franks et al. 2001, Hughes and Boomsma 2007, Jaffé et al. 2007, Kronauer 2020; Fig. 1B). This can be conceptualized as diverse, genetically determined reaction norms overlapping at the level of the individual, which helps group-level adaptation of the colony phenotype to its environment (Hughes and Boomsma 2007). Worker caste development can be understood as becoming increasingly more 'queen-like' with increasing size (Trible and Kronauer 2017; Fig. 1B). Because morphological adaption occurs during early development, before individuals are put to work, the predictability of future environmental conditions is a key factor in favoring a plastic or constrained reaction norm. If the environment varies rapidly and unpredictably, the slow, irreversible consequences of a developmental response could result in traits that are poorly matched to conditions (DeWitt and Scheiner 2004). In contrast, within such environments, rapidly adjusting and reversible behavioral plasticity is more likely to allow for an adaptive set of trait outcomes. Such plasticity is expected to evolve when individuals 1) are sufficiently exposed to changeable conditions, 2) can obtain reliable information about the state of the environment, and 3) are able to respond within a relevant timeframe (DeWitt et al. 1998, Gabriel et al. 2005).

Morphologically differentiated castes are an eye-catching hallmark of superorganismal functional heterogeneity, but behavioral plasticity, such as in task allocation, is even more ubiquitous. Social insects are highly sensitive to cues and signals provided by the colony and outside environment, adjusting their task specialization to adapt to changing work needs (Robinson et al. 1997, Smith et al. 2008). A prime example of this can be observed in the worker activity of the rock ant *Temnothorax albipennis* (Curtis 1854) (Hymenoptera: Formicidae) (Fig. 1C), with an 'elite' performing much of the work for a given task; yet following their removal, task allocation is sufficiently plastic to reallocate previously less active workers (Pinter-Wollman et al. 2012b). Importantly, for many species, the shift in activity patterns engendered by such perturbations is reversible, as work demands continue to change (Huang and Robinson 1992, Herb et al. 2012). Furthermore, differences between animal group members may also include differences in plasticity per se (Dingemans and Wolf 2013). Thus, even if behaviorally plastic individuals all experience the same environmental changes, their behavior will adapt differently. For instance, differences in the plasticity of task allocation have been observed in honey bees (Giray and Robinson 1994). Interindividual differences in behavioral plasticity may result from differences in state variables (e.g., energy levels; Mathot et al. 2011). They may also result from spatial and temporal variation in the environment, for example in food patches, where plasticity in sampling behavior could be beneficial, with a negative frequency dependence (DeWitt et al. 1998, Wolf et al. 2008). Additionally, given the existence of individual differences, a capacity to adjust behavioral strategies following social interactions would seem to be fitness-enhancing (McNamara and Leimar 2010). These three explanations are nonexclusive, and may each contribute to individual variation in plasticity (Dingemans and Wolf 2013).

In a similar fashion to development, plasticity in behavior has been described using the concept of behavioral reaction norms (Dingemans et al. 2010). This helps to reconcile the idea of animal

‘personality’, which relates to consistent behavioral differences between individuals (Sih et al. 2004, 2012; Réale et al. 2007), and adaptation to the environment. Such differences may contribute to within-caste task allocation, and fine-scale variation in monomorphic workers. For example, some honey bee workers are found to be more socially interactive than others, which may contribute to behavioral specialization through learning (Walton and Torh 2016; Fig. 1A). Further examples of behavioral variation within social insect colonies are numerous (Jandt and Gordon 2016). Superorganisms can themselves be considered as ‘individuals’, and correspondingly the idea of collective, or colony-level, personality is increasingly prominent in social insect research (Chapman et al. 2011, Bengston and Jandt 2014, Jandt et al. 2014, Cronin 2015). Notably, *Temnothorax* ant colonies are found to vary in aggression (Scharf et al. 2012) and risk preferences (Bengston and Dornhaus 2014), whereas collective personalities in honey bee colonies have been empirically linked to colony fitness (Wray et al. 2011). A combination of genetics, physiology, and environment are thought to influence the development of such colony-level differences (Pinter-Wollman et al. 2012a, Jandt et al. 2014), though the interplay of these factors is, per se, an active topic of research. There is also evidence that collective personalities themselves can be flexible. For example, colonies of the leafcutter ant *Atta colombica* (Guérin-Méneville 1844) (Hymenoptera: Formicidae) are observed to become more aggressive, threat responsive, and phototactic within 2 wk of disturbance, thus demonstrating a shift in several behavioral traits, in response to a single specific stimulus (Norman et al. 2017).

Social insect superorganisms are well-placed to elucidate the role of phenotypic plasticity in generating adaptive heterogeneity in animal collectives. This is not only because they can be tractably deconstructed and manipulated, but because they often show strong responses to changing environmental conditions. Their utility is further complemented by the study of transitional eusocial insect societies, such as those of *Polistes* (Latreille 1802) (Hymenoptera: Vespidae) paper wasps, in which individuals retain the ability to switch between reproductive and nonreproductive phenotypes as adults (Sumner et al. 2006, Gotoh et al. 2008, Patalano et al. 2015, Kennedy et al. 2017). Insights into the role of phenotypic plasticity in generating functional heterogeneity will have relevance far beyond the social insects. For example, social spiders (Hunt et al. 2019), cockroaches (Planas-Sitjà et al. 2015), and stickleback fish (Jolles et al. 2017) have all been observed to have collective behavior that is shaped by individual differences. Future research directions include the questions of: how intra- and intercolony variation is developed and maintained; how collective personalities emerge from a distribution of individual personalities; and how personality types relate to task allocation. In addition to complementary insights from other social taxa, advancements in epigenetic manipulation (Yan et al. 2014), artificial colony formation (Warner et al. 2018), and remote sensing technology (Pérez-Escudero et al. 2014) will help to elucidate the role of behavioral plasticity in the dynamics of superorganismal function.

The Costs and Benefits of Group Diversity

Social insects are well known for their intragroup diversity and extremely efficient collective behavior (Hölldobler and Wilson 1990, 2009). The allocation of tasks—workers may specialize in certain tasks, such as brood care or foraging—is probably the most significant feature of social insect success (Usher et al. 1979, Sendova-Franks and Franks 1993, Bourke and Franks 1995). Studies have also reported beneficial effects of different kinds of intracolony diversity, such as genetic, behavioral, and morphological variation (Usher et al. 1979, Hölldobler and Wilson 2009, Jandt et al. 2014,

Jeanson and Weidenmüller 2014). However, although the putative advantages of heterogeneity have received much attention, relatively less research has been devoted to elucidating its potential costs (Van Baalen and Beekman 2006, Jeanson and Weidenmüller 2014). Here, we examine both the costs and benefits of heterogeneity in social insects, and their wider implications.

In certain cases, the benefits of interindividual heterogeneity can be directly quantified. For example, genetically diverse colonies of the honey bee *A. mellifera* exhibit enhanced productivity, such as higher foraging rates and greater amounts of food storage, and increased longevity when compared with genetically uniform ones (Mattila and Seeley 2007). Furthermore, in colonies of the acorn ant *Temnothorax longispinosus* (Roger 1863) (Hymenoptera: Formicidae), intracolony variance in aggression is positively correlated with efficiency of task allocation and colony productivity (Modlmeier and Foitzik 2011). Morphological differences within colonies of the fire ant, *Solenopsis invicta* (Buren 1972) (Hymenoptera: Formicidae), also increase brood production, especially when food is scarce (Porter and Tschinkel 1985). At the level of decision-making, again in the honey bee *A. mellifera*, colonies composed of foragers that vary widely along the speed-accuracy axis—fast but inaccurate, or slow but accurate—have better responses to environmental fluctuation (Raine and Chittka 2012).

Although research has frequently shown the benefits of diversity, its negative effects on collective performance in social insects have also been reported (Jeanson and Weidenmüller 2014). For example, worker size variation impairs efficiency of communication in the stingless bee genera *Melipona* (Illiger 1806) (Hymenoptera: Apidae) and *Trigona* (Jurine 1807) (Hymenoptera: Apidae) (Waddington et al. 1986) and the honey bee, *A. mellifera* (Waddington 1989). Moreover, when queens of the bumble bee, *B. terrestris*, are artificially inseminated with sperm from one male, related males, or unrelated males, colony fitness follows a U-shaped function, with minimum fitness levels for small amounts of genetic variation. This finding suggests that the relationship between diversity and collective performance is not always monotonically positive, or linear in nature (Baer and Schmid-Hempel 2001). Although such costs have received less attention when compared with fitness benefits, it has been argued that they are equally important in understanding the evolution of intracolony diversity (Van Baalen and Beekman 2006, Jeanson and Weidenmüller 2014). Factors such as genetic conflict, an increased need for worker policing, and the cognitive constraints of behavioral flexibility, constitute additional notable examples. As such, the trade-offs of these potential costs with the benefits of heterogeneity will need to be taken into account in future investigations (Jeanson and Weidenmüller 2014).

How does diversity among colony members influence collective performance? Surprisingly, the exact mechanisms are still largely unknown. Task specialization is often believed to increase colony performance, because specialized workers more efficiently conduct their tasks than do others (Usher et al. 1979, Robinson 1992, Sendova-Franks and Franks 1999, Jandt et al. 2014, Jeanson and Weidenmüller 2014). However, this idea has rarely been empirically demonstrated (Wilson 1987, Beshers and Fewell 2001, Tschinkel 2013), and some studies have actually found that in certain cases, specialized workers are no more efficient at their tasks than others (Dornhaus 2008, O’Shea-Wheller et al. 2016). Similarly, a number of studies have demonstrated positive effects of intracolony diversity on collective decision-making using theoretical models or computer simulations (Masuda et al. 2015; Hasegawa et al. 2017, 2020; Valentini et al. 2020), but their assumptions are often difficult to test using real animals, because this typically requires fine-scale

individual data of behaviors and interactions, specifically in ecologically relevant settings. As such, many of the emergent processes that give rise to collective behaviors as a consequence of diversity among colony members, require further empirical investigation.

Future research should consider applying novel technologies to colonies, while exploring new model systems, both to reveal previously unknown benefits and costs of group diversity, and the underlying mechanisms driving these emergent processes in social insects. Thanks to recent advances in monitoring technology, automated tracking systems have become a rapidly evolving tool to do so (Crall et al. 2015, Yamanaka and Takeuchi 2018, Nath et al. 2019, Sridhar et al. 2019). Notably, these provide the opportunity both to track individual workers in detail, while simultaneously monitoring a large number of colony members at once. Using such cutting-edge tools, researchers have begun to reveal novel collective phenomena in social insects. For example, a recent study has shown that social network plasticity decreases disease transmission in colonies of *Lasius niger* (Hymenoptera: Formicidae) ants (Stroeymeyt et al. 2018). Furthermore, there is ongoing potential to manipulate genetic, morphological, and behavioral diversity within certain tractable social insect colonies (Jeanson and Weidenmüller 2014). Thus, using social insects as model systems, researchers can develop hypotheses relating to functional heterogeneity, based on detailed individual data, and then empirically test these hypotheses by modifying group compositions. Future research can hence examine both the proximate causes, and ultimate consequences, of group diversity, and in turn develop novel theories to build a deeper understanding of functional heterogeneity.

Functional Heterogeneity and Bioinspiration

Social insect superorganisms live in almost every habitat type and tackle varied ecological challenges (Schultz 2000). As such, the application of colony behaviors and heuristics to engineered systems, is a promising area of research (Bonabeau et al. 1999). We have thus far discussed the myriad forms and functions of heterogeneity in social insect colonies (Fig. 1), and here we highlight where these can contribute to bioinspiration in engineering. Bioinspiration is the practice of adopting solutions and materials present in biological systems, which have necessarily been honed by the action of natural selection, and utilizing them to solve challenges in applied science and engineering (Sanchez et al. 2005).

Designing emergent and adaptive multiagent systems has been a goal of engineering for some years (Matarić 1993, 1995), but de novo system design is challenging. Consequently, superorganisms are a prime source of inspiration in engineering large distributed systems, or in techniques to solve complex mathematical problems. Notable examples include swarm robotics (Şahin 2005, Hamann 2018) and ant colony optimization (Dorigo and Di Caro 1999, Dorigo and Blum 2005), which exploits the notion of swarm intelligence (Smith 2005). Increasingly, there is also recognition that superorganisms ‘anticipate’ technologies, such as the Transmission Control Protocol, used to manage congestion in internet data traffic (Prabhakar et al. 2012), and Markov chain Monte Carlo methods used to sample from probability distributions (Baddeley et al. 2019, Hunt et al. 2020). Thus, as biologists better understand how superorganisms self-organize, the more immediate is the potential for bioinspired technological breakthroughs, and enhancements to existing techniques. Swarm biology and engineering meet at a common interface of mathematical models (Smith 2005, Hamann and Schmickl 2012); and thus model-driven empirical research of

functional heterogeneity in superorganisms, has scope for considerable technological, as well as a scientific, impact.

One common aim for swarm systems is that they should be robust to the loss or partial failure of agents, and yet there is rising awareness that fault tolerance may be limited in large groups (Bjerknes and Winfield 2013). Biological swarms, however, would seem to be necessarily error or noise tolerant as a matter of course, because there is an inevitable level of genotypic and phenotypic variability, in contrast to engineered swarms, that are most commonly homogeneous (Hamann 2018, Schranz et al. 2020). This is a relic of the classical engineering paradigm that sees variation among system components as unwelcome noise to be minimized (Dorigo et al. 2013). Understanding the mechanisms of cooperation between somewhat diverse colony members, could thus contribute to more robustly engineered swarms, and has been the focus of work such as the ‘Swarmanoid’ project (Ducatelle et al. 2010, 2011; Ferrante et al. 2012; Fig. 1D). Indeed, the importance of phenotypic plasticity to insect superorganisms (Kennedy et al. 2017) suggests that it constitutes one of the essential components required to bring robots from the laboratory into the field (Hunt 2020).

A notable example of adaptive interindividual diversity is the ability of more genetically diverse ant colonies to better respond to pathogens (Ugelvig et al. 2010). This points to the possibility that more diversely engineered swarms could be harder to subvert; which is important, as swarm security is an emerging area of research (Higgins et al. 2009). Another key aspect of robot swarm development is the need for collective decision-making capabilities; as this is necessary for long-term autonomy. Decision-making has been demonstrated in large swarms using homogeneous behaviors (e.g., (Valentini et al. 2016)); however, diversity in option acceptance thresholds, or assessment behavior, as is seen in social insects, could facilitate further improvements in real-world decision-making efficiency (Masuda et al. 2015, O’Shea-wheller et al. 2017). This can be exemplified by the collective nest choice behavior of the ant *T. albigipennis*, in which workers appear to display varying nest acceptance thresholds, ensuring that superior options are preferentially chosen, without the need for direct comparisons (O’Shea-wheller et al. 2017) (Fig. 1C). It should be noted that such systems are distinct from cases where heterogeneity among individuals acts only as a tool for the elimination of error, as seen in some ‘collective intelligence’ scenarios in humans, where independence of error causes extreme values to effectively cancel each other out (Galton 1907, Treynor 1987, Chen et al. 2014), and similar accuracy is required among group members (Kurvers et al. 2016). Instead, they represent cases in which diversity itself imparts emergent forms of functionality via system flexibility, thus providing novel solutions to classic problems (Jones et al. 2004, Masuda et al. 2015). Indeed, the use of heterogeneous activation thresholds has been shown to generate effective task allocation in small robot groups, even under noisy conditions (Krieger and Billeter 2000), thus the expansion of this concept into decision-making seems technically feasible.

The case of enhanced homeostasis in genetically diverse social insect colonies (Jones et al. 2004, Oldroyd and Fewell 2007), points toward the general advantage of a system of having the capacity to take on different states in its response to perturbations (e.g., a proportion of workers engaged in cooling behaviors, rather than all being activated at once). This was formulated by the cybernetics pioneer W. Ross Ashby as the ‘Law of requisite variety’ in 1958 (Ashby 1958): in a multi-agent system, the greater the variety of actions available, the greater the variety of disturbances that can be compensated for (Parunak et al. 2004, Campbell et al. 2011). Examples of algorithmic diversity benefiting the performance of engineered

systems have been noted in smart camera networks, particle swarm optimization, and web server load balancing (Lewis et al. 2014). However, there is relatively little work in artificial systems to demonstrate how the distribution of response thresholds affects task performance (see Campbell et al. 2011). Recent simulation work finds that a uniform distribution of thresholds in a computational task allocation problem outperforms a homogeneous constant, as well as Gaussian and Poisson distributions (Wu et al. 2020). Although biological simulations often assume normally distributed reaction thresholds (Graham et al. 2006), further model-driven experimental work on a variety of colony task allocation problems would be valuable to verify that this is more than a convenient modeling assumption. The combined action of genotypic diversity and phenotypic plasticity acting throughout individuals' lifetimes, in environments that are heterogeneous in time and space, may tend to result in more complex distributions. As such, understanding whether and how this is functionally significant will be valuable in a range of applied science and engineering contexts.

Conclusion

The field of social insect research presents ongoing potential for significant conceptual and methodological advances in the study of basic biology. However, the understanding of functional heterogeneity in insect colonies is still far from comprehensive, largely as a result of its inherent complexity. Functional heterogeneity is not unique to social insects but instead exists as a pervasive facet of biological processes. As such, by examining the form and function of heterogeneity within insect colonies, there is scope for considerable impact in adjacent fields, including network science, and the study of emergent systems. By virtue of their modular organization, insect superorganisms continue to serve as a valuable interdisciplinary tool for the characterization of functional variation, and its evolutionary significance. Important future work includes the continued development of insect models that enable precise manipulation of traits and behavioral propensities; the linking of genetic, behavioral, and physiological variation to group-level outcomes; and exploration of how heterogeneity at different levels of organization interacts, and is maintained. Investigations will benefit from emerging methodologies, such as long-term computer tracking of individuals, and in vivo gene editing. Taken together, this research will further demonstrate the phenomenon of functional heterogeneity in social insects to be paradigmatic for understanding fundamental mechanisms in biology, and complex adaptive systems.

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Conflict of Interest

The authors declare that they have no competing interests.

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