



## How to become one: the proximate mechanisms of self-assembly behaviour in social insects (Hymenoptera: Formicidae, Apidae)

Daniele CARLESSO & Chris R. REID

### Abstract

Collective behaviour is an integral part of social insects' lives. From nest building to complex foraging networks, insects have evolved extraordinary abilities to organize and coordinate their actions to solve challenges outside the reach of the capabilities of an individual. One of the most striking examples of collective behaviour observed in social insects is that of self-assemblages: sophisticated three-dimensional structures that insects form by linking their bodies together. Self-assemblages are extremely dynamic, can rapidly adapt to colony needs and local conditions, and rapidly disassemble when no longer needed. As other forms of collective behaviour, these structures are completely self-organized. They emerge from relatively simple and locally mediated interactions among colony members, which are only locally informed and without any blueprint. Research on the proximate mechanisms underlying the emergence of self-assemblages has long been hindered by their inherent complexity. In the last twenty years, however, increased access to advanced technological tools has allowed scientists to describe the individual-level rules used by insects when self-assembling. Here, we review the current knowledge on the behavioural rules governing self-assembly behaviour in social insects, highlighting the striking similarities observed within and among genera. We discuss the impact that two factors – inter-individual heterogeneity and environmental geometry – may have on self-assemblages and suggest these as promising areas for future research in the field. Lastly, we propose a simplified algorithm for self-assembly behaviour in the two ant genera for which we have the most individual-level data – *Eciton* army ants and *Solenopsis* fire ants – showing that a few behavioural rules can be generalised to multiple structures. Further research on the proximate mechanisms underlying self-assemblages is necessary to understand the evolutionary history of this behaviour in insect societies and to provide insights to engineers and roboticists for developing adaptive algorithms for artificial swarm systems.

**Key words:** Collective behaviour, self-organisation, ants, honey bees, swarm behaviour, emergence, behavioural algorithms, review.

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### Introduction

In 1874, American naturalist Thomas Belt reported the striking self-assembly behaviour of *Eciton* army ants: “Another time they were crossing a water-course along a small branch [...] They widened this natural bridge to three times its width by a number of ants clinging to it and to each other on each side, over which the column passed three or four deep. Except for this expedient they would have had to pass over in single file, and treble the time would have been consumed. Can it not be contended that such insects are able to determine by reasoning powers which is the best way of doing a thing, and that their actions are guided by thought and reflection?” (BELT 1874). As other scientists of the time (SELOUS 1901), Belt interpreted the coordination observed in animal groups as the result of

high cognition and / or planning abilities. Since then, the study of animal collective behaviour took a turn thanks to the introduction of the principles of self-organisation into the field by Jean-Louis Deneubourg and contemporary colleagues (DENEUBOURG & GOSS 1989, BONABEAU & al. 1997, CAMAZINE & al. 2001, SUMPTER 2006). Adopting principles from control theory (ASHBY 1947), self-organisation is the process by which complex group-level patterns emerge from repeated and locally-mediated interactions among members of the group (CAMAZINE & al. 2001). This means that animals do not need to possess knowledge about the global state of the system and must only react to stimuli available locally to generate the observable collective patterns. The principles of self-organisation have since been

widely applied to describe and simulate the behaviour of the most diverse animal groups (COUZIN & KRAUSE 2003, SUMPTER 2006), including schools of fish (KATZ & al. 2011, MACGREGOR & al. 2020), insect aggregations (BONABEAU & al. 1997, BUHL & al. 2006), flocks of birds (HILDENBRANDT & al. 2010, PAPADOPOULOU & al. 2022), and human crowds (MOUSSAÏD & al. 2010, WARREN 2018).

One of the most spectacular examples of collective behaviour in animal groups is that of the self-assemblages in social insects: highly functional structures that insects form by linking their own bodies together (ANDERSON & al. 2002). Examples of these structures are the bridges and scaffolds of *Eciton* army ants (Fig. 1B) (GARNIER & al. 2013, REID & al. 2015, LUTZ & al. 2021, MCCREERY & al. 2022), the chains formed by *Oecophylla* ants (Fig. 2A and 2B) (LIONI & al. 2001), and the swarm clusters that *Apis* bees use for nesting during colony emigrations (Fig. 3A) (HEINRICH 1981b, DYER & SEELEY 1991, SEELEY 2010). Self-assemblages can span several times the size of the insects composing them, are incredibly adaptive to changes in the surrounding environment, and quickly disassemble when no longer needed. Analogously to all other forms of collective behaviour, the formation of self-assemblages is underlain by simple interaction rules followed by individuals that only possess local information (CAMAZINE & al. 2001, SUMPTER 2006).

In a seminal review on the topic, ANDERSON & al. (2002) described the function of self-assemblages in the lives of social insect colonies and highlighted the scarcity of knowledge about the proximate mechanisms (behavioural rules and local stimuli) that underlie the formation of these structures. These mechanisms have in fact been elusive due to inherent properties of self-assemblages: extreme density of individuals, occlusion of the internal architecture, high volume of movement within the structures, and rapid disassembly when disturbed. In the last two decades, the study of self-assemblages has rapidly progressed thanks to the shift from fieldwork to controlled laboratory conditions and to the wider availability of advanced technological tools in research. High resolution video recordings and computer vision allow scientists to rapidly extract data on the global state of the structures, while being able to track the behaviour of individual insects within and over the structure. Accessibility to x-ray computer-tomography (CT) scanning has recently allowed the analysis of the internal architecture of some self-assemblages (SHISHKOV & al. 2022), once inaccessible without disturbing the insects or confining the structure in unnatural conditions. Further, advances in computer technology opened up the possibility of running complex mathematical models for validating the behavioural rules extracted experimentally and generating testable predictions on the dynamics of the structures. These tools have aided researchers in discovering the proximate mechanisms governing the emergence of self-assemblages in insect groups.

The scope of this review is to summarise our knowledge on the behavioural rules that insects use when self-assem-

bling into functional structures and to highlight promising areas of research in the field. In the first section, we review the local stimuli that insects react to when making decisions about joining, leaving, or remaining in the structure, highlighting striking similarities observed across species and structures. We divide the local stimuli available to insects in two main categories – social and environmental – to isolate the basic mechanisms that underpin self-assemblage formation in different species. We define any information that an insect receives from nestmates as social and any stimulation originating from other sources as environmental. We then discuss the role of structural weight in determining the final configuration of self-assemblages. Dissimilar from other kinds of collective behaviour, indeed, insects within structures are physically connected to each other and must sustain the load of other individuals for long periods of time. We overview the behavioural mechanisms that are available to insects to avoid getting injured while preserving the structural integrity of the self-assemblages. Finally, in the second part of the review, we explore two areas of research seldom investigated to date. We first discuss the role of environmental geometry in shaping self-assemblages. We suggest that different structures may emerge from the same set of behavioural rules when applied in different environmental contexts and propose self-assemblages as a unique model system to study the feedback loops emerging from the interactions between insects and the environment. We then focus on the impact of individual heterogeneity on self-assembly formation. Inter-individual variation has recently been explored in other forms of collective behaviour (COOK & al. 2020, JOLLES & al. 2020) and may play a critical role for the optimisation and efficiency of self-assemblages (POWELL & FRANKS 2007, PURCELL & al. 2014, KRONAUER 2020). Lastly, we highlight promising future directions of research that will improve our understanding of the mechanisms behind self-assembly formation in social insects.

## What do we know about the proximate mechanisms of self-assemblages?

### Social information

Inter-individual interactions among group members are the backbone of collective behaviour, and self-assembly is no exception. In this section we divide social interactions in two main categories: tactile stimulation and pheromonal communication. The former refers to direct interactions among nestmates involving physical contact and is primarily inhibitory, whereas pheromone signals are a form of indirect communication that can promote or halt the formation of self-assembly by coordinating the aggregation among individuals.

**Tactile stimulation:** The ability to perceive and react to tactile cues provides insects with a robust local mechanism to assess their usefulness in the structure and modulate their behaviour accordingly. In self-assembly literature, tactile stimulation is commonly interpreted



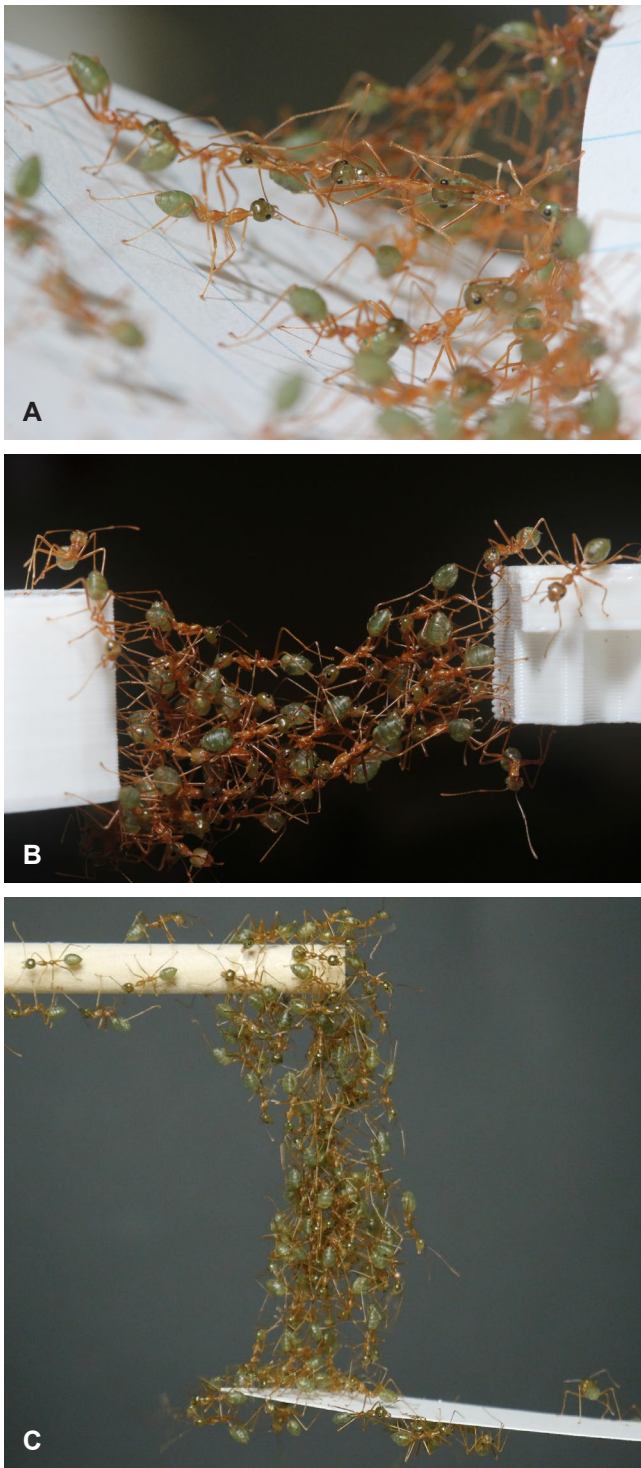
**Fig. 1:** Depiction of the self-assemblages built by epigeal *Eciton* army ants. A) Bivouac, B) scaffold, C) bridge, D) plug. Image credits: A) All rights reserved © Daniel Kronauer, Rockefeller University (NY, USA); B) All rights reserved © Chris R. Reid, Macquarie University (Sydney, Australia); C) All rights reserved © Chris R. Reid, Macquarie University (Sydney, Australia); D) All rights reserved © Alex Wild. All images used by permission or under CC license.

as the rate of physical interaction among nestmates. Individuals participating in self-assemblages can estimate the localised traffic flow passing over them and decide to leave only when this stimulation terminates or drops below a critical threshold (POWELL & FRANKS 2007, MLOT & al. 2011, GARNIER & al. 2013, PHONEKEO & al. 2017, MCCREERY & al. 2022). This behavioural rule – which has often been translated as “don’t move if someone is on top of you” (MLOT & al. 2011, PHONEKEO & al. 2017) – is thought to underlie the striking adaptiveness of self-assemblages to local traffic and rapidly changing conditions.

Workers of *Eciton* army ants use tactile stimulation to decide whether to stop and plug potholes encountered along the foraging trails (Fig. 1D) (POWELL & FRANKS 2007). Ants that decided to plug a pothole only leave their position when the traffic flow over them stops for more than five seconds. Strikingly, GARNIER & al. (2013) simulated bridge formation using the same behavioural rule (Fig. 1C). The ability of army ants to keep track of local traffic for five seconds makes bridges akin to a buffered system – that is, they reduce the impact of temporary declines in traffic: Bridges are extremely stable despite fluctuations in traffic flow, yet they can rapidly disassemble if traffic is interrupted. Although not explicitly tested, it is likely that tactile cues modulate the time that ants spend motionless after slipping when forming scaffolds

over inclined surfaces (Fig. 1B, Tab. 1) (LUTZ & al. 2021). Responsiveness to tactile stimulation is also pivotal for the cohesion and stability of the self-assemblages of *Solenopsis* fire ants, which routinely form floating rafts (Fig. 4A) and temporary nests (“towers”) (Fig. 4C) to survive the flooding of their natural habitat (ADAMS & al. 2011, MLOT & al. 2011, PHONEKEO & al. 2017). Rafts are floating structures composed of a layer of structural ants in contact with water, which are kept motionless by a layer of freely moving individuals walking on top of the structure (MLOT & al. 2011). The continuous tactile stimulation provided by freely walking individuals is necessary to maintain raft cohesion, as demonstrated by the rapid replacement of these ants by structural individuals if they are experimentally removed from the structure. This behavioural rule has also been applied for simulating tower building in the same species of ants, indicating that the inhibitory stimulation provided by tactile cues plays a central role in the formation of these structures (PHONEKEO & al. 2017, NAVE Jr & al. 2020). The generalisability of the same behavioural rule to the production of multiple self-assemblages strongly suggests that ants may not need to change their behaviour depending on the environmental context.

While the presence of tactile stimulation boosts structural stability, its absence can drive changes in the structure and promote adaptation to the surrounding environment.



**Fig. 2:** Depiction of the self-assemblages built by *Oecophylla* ants. A) Pulling chain, B) bridge, C) hanging chain. Image credits: A) All rights reserved © Chris R. Reid, Macquarie University (Sydney, Australia); B) All rights reserved © Chris R. Reid, Macquarie University (Sydney, Australia); C) Daniele Carlesso, Macquarie University (Sydney, Australia). All images used by permission or under CC license.

Army ants' bridges remain in place for as long as needed, yet quickly disassemble when traffic flow is interrupted (GARNIER & al. 2013). This simple behavioural rule allows

army ants to efficiently form structures where needed and avoid locking individuals into structures when traffic is deviated (POWELL & FRANKS 2007). Differences in the amount of traffic flow on the two sides of a bridge may even cause the bridge to move across a gap and create a shortcut in the foraging trail (REID & al. 2015). The movement of the bridge originates from the interplay between pheromone trail dynamics and responsiveness to tactile cues: pheromone-following ants seeking the shortest available path generate higher traffic volume on the inner side of the bridge, thereby increasing the tactile stimulation experienced by structural ants occupying that position and, in turn, inhibiting their movement. At the same time, ants on the outer edge of the bridge are more likely to leave their positions because they experience less traffic flow over them. The decrease of traffic along the outer edge of the structure, paired with an increased pheromone deposition rate along the inner side, facilitates the movement of the bridge across a gap and the emergence of a shortcut along the trail (REID & al. 2015, GRAHAM & al. 2017). The final position of the bridge is then determined by the interaction between traffic flow and environmental geometry (GRAHAM & al. 2017). Similar feedback loop dynamics have been found in the rafts formed by *Solenopsis* fire ants (WAGNER & al. 2021). These examples showcase how a simple behavioural rule – “don't move if others are on top of you” – interplays with the surrounding environment and allows social insects to rapidly adapt to various environmental contexts.

**Pheromones:** Pheromonal communication plays a vital role in coordinating activity within social insect colonies, allowing the rapid broadcast of information to several group members (VANDER MEER & al. 1998, JACKSON & RATNIEKS 2006, NGUYEN & al. 2021). Some pheromones promote clustering of individuals in certain areas, thereby increasing the frequency of interactions among nestmates and their likelihood of forming a structure. This form of communication has thus the potential to indirectly impact the formation and maintenance of self-assemblages by modulating the interactions among insects.

Pheromone trails building up over an army ants' bridge enhance the structure's stability by increasing traffic flow and, in turn, the tactile stimulation perceived by structural individuals (POWELL & FRANKS 2007, GARNIER & al. 2013, REID & al. 2015). As mentioned in the previous section, the interaction between pheromone trail dynamics and ants' responsiveness to tactile cues can lead to the movement of a bridge across a gap and therefore the creation of shortcuts on a trail (REID & al. 2015, GRAHAM & al. 2017). In both cases, pheromone trails reinforce structural stability by mediating the interactions among individuals. While not yet tested, it is likely that alarm pheromones may broadcast the presence of danger to the group and trigger rapid disassembly of structures.

In honey bees of the genus *Apis*, self-assembly behaviour is mediated by the emission of pheromones that coordinate the clustering of individuals around relevant targets (VANDER MEER & al. 1998). For example, when a



**Fig. 3:** Depiction of the self-assemblages built by *Apis* bees. A) Swarm cluster of *Apis mellifera*, B) bee curtain of *Apis dorsata*, C) festoon, D) anti-predatory ball of *Apis cerana* against *Vespa mandarinia japonica* (visible in orange). Image credits: A) Steven dosRemedios; B) Public Library of Science One; C) Maja Dumat; D) Masato Ono, Tamagawa University (Tokyo, Japan). All images used by permission or under CC license.

hornet attacks a nest, the emission of the alarm pheromone isopentyl acetate coordinates workers to cluster around the attacker and kill it (Fig. 3D) (BARACCHI & al. 2010, TAN & al. 2016). *Apis* bees also use pheromones to maintain cohesion during colony emigrations. Nasonov scenting attracts individuals to gather around the queen and form swarm clusters (Fig. 3A) (MORSE 1963, AVITABILE & al. 1975, WINSTON & al. 1989, NGUYEN & al. 2021). Clusters are held together by a combination of Nasonov scenting and queen mandibular pheromones, and they only disassemble once a new nesting cavity is selected through a sophisticated decision-making process (SEELEY & al. 1991, SEELEY & BUHRMAN 1999, SEELEY 2010).

### Environmental stress

Self-assembly differs from other examples of collective behaviour in that group members are linked to each other through physical connections. Individuals participating in self-assemblages have to sustain the weight of their nest-mates, and they may need to rearrange their inter-individual connections to avoid excessive loads that may injure them. Some self-assemblages, such as the swarm clusters of honey bees or the rafts of fire ants, are built in delicate

moments in the colony's life. These structures must also be able to resist mechanical perturbations caused by wind, rain, or other adverse weather events, and failure to do so may lead to the death of the colony. Further, structures persisting for several days in the open may need thermoregulation to ensure optimal brood development and adequate workers' activity levels. In the following section, we review the behavioural rules that allow insects to maintain colony cohesion and structural integrity in spite of adverse environmental conditions.

**Exogenous mechanical perturbations:** Environmental perturbations such as wind or vibrations can induce strong mechanical strains on self-assemblages, putting their structural integrity at risk. Some self-assemblages show large morphological changes in response to mechanical stress (MLOT & al. 2011, TENNENBAUM & al. 2016, PELEG & al. 2018). These changes enhance the mechanical stability of the assemblage (PELEG & al. 2018) and prevent individuals in the structure from getting injured (TENNENBAUM & al. 2016, PHONEKEO & al. 2017). The mechanical state of fire ants' aggregations switches between solid-like and fluid-like as a function of the applied force (HU & al. 2016, TENNENBAUM & al. 2016, TENNENBAUM



**Fig. 4:** Depiction of the self-assemblages built by *Solenopsis invicta* ants (A and C), *Formica selysi* ants (B), and *Leptogenys cyanicatena* ants (D). A) floating raft of *S. invicta* ants, B) floating raft of *F. selysi* ants, C) tower of *S. invicta* ants, D) pulling chains formed by *L. cyanicatena* to transport large millipede. Image credits: A) Brant Kelly; B) D. Galvez; C) Royal Society Publishing; D) All rights reserved © Stephane De Greef. All images used by permission or under CC license.

& FERNANDEZ-NIEVES 2017, VERNEREY & al. 2018). The transition between states originates from the ability of ants to rearrange their leg connections with neighbouring individuals (FOSTER & al. 2014, TENNENBAUM & al. 2016, VERNEREY & al. 2018, TENNENBAUM & FERNANDEZ-NIEVES 2020). Structural ants estimate the local strain magnitude through the stretching of their leg connections and use this information to rearrange their connectivity (TENNENBAUM & al. 2016, VERNEREY & al. 2018). The rate at which this rearrangement occurs determines the mechanical state of the aggregation. When a stress is applied at a rate faster than that of the leg rearrangement, the aggregation stores energy through the elasticity of the leg connections and returns to its original state when the stress terminates. When the perceived strain exceeds a certain threshold, however, ants rearrange their connections with neighbouring individuals and the behaviour of the aggregation switches to that of a fluid (VERNEREY & al. 2018). From a biological perspective, the ability to switch between mechanical states is likely to help ants maintain cohesion while rafting and tower building. When rafting, ants must be able to withstand frequent transient stresses caused by water currents or rain without detaching from each other

(MLOT & al. 2011). Then again, the ability to rearrange connections ensures that individuals do not suffer excessive loads when forming towers (TENNENBAUM & al. 2016, PHONEKEO & al. 2017).

The ability to maintain cohesion under mechanical stress largely depends on the stimuli that insects can perceive and react to. The shift in mechanical state exhibited by fire ant aggregations emerges from ants' ability to locally assess the strain applied on the aggregation through the stretching of their legs (TENNENBAUM & al. 2016, VERNEREY & al. 2018). Understanding what local information is available to individuals in the structure is central when investigating the mechanisms underlying the functional adaptations of self-assemblages. The swarm clusters formed by honey bees rapidly flatten in response to large horizontal oscillations, but they fail to do so when the structure is shaken vertically (PELEG & al. 2018). Flattened clusters are more mechanically stable than elongated ones, greatly reducing the load perceived by bees in the structure and decreasing the probability of structural failure. The morphological change is guided by the selective response of bees to an increase in local normal strains (e.g., relative displacement). Horizontal shaking causes clusters to swing

from side to side, generating large local strains in the areas of the structure connected to an external support (i.e., a tree branch) (Fig. 3A). Once these strains exceed a certain threshold, bees start moving from areas of low strain (i.e., the tip of the structure) to areas of high strain (i.e., closer

to the external support). The coordinated movement of the bees towards the base of the structure causes the flattening of the cluster and a reduction in the normal strains perceived by bees. Vertical shaking, however, does not generate normal strains large enough to trigger this reaction,

**Tab. 1:** Summary of the currently known social insect self-assemblages by function (first column). For each structure, we report: 1) species in which it is found, 2) environmental context triggering its formation, 3) individual-level trigger for self-assembling, 4) individual-level stimuli available to insects when self-assembling, 5) brief description of its architecture, and 6) the functional adaptations that it shows. Words in parentheses indicate hypothesised mechanisms that are likely but not yet tested.

Function	Structure	Species	Environm. context	Trigger	Individual-level stimulation	Description	Functional adaptations	References
Nesting	Towers	<i>S. invicta</i>	Shore reaching after rafting	(N/A)	Tactile stimulation, Load sustained	Several layers of workers around a central vertical support, may contain brood	Waterproofing	PHONEKEO & al. (2017), NAVE & al. (2020)
	Bivouacs	<i>E. hamatum</i> , <i>E. burchellii</i>	Colony emigration, Nest	(Increased interaction rate), (Darkness)	(Load sustained), (Tactile stimulation), (Queen / Brood pheromones), Temperature	Cluster of individuals, organized in hanging chains connected laterally and at the bottom, contains brood	Thermoregulation, (Waterproofing)	SCHNEIRLA & al. (1954), FRANKS (1989), BAUDIER & al. (2019), BOCHYNEK & al. (2021)
	Swarm clusters	<i>A. mellifera</i> , <i>A. cerana</i> , <i>A. dorsata</i> , <i>A. florea</i>	Colony emigration	Gradients of distance from queen pheromone, Nasonov scenting	Queen pheromone, Nasonov pheromone, Load sustained, Local normal strain, Temperature	Cluster of individuals, organised in hanging chains connected laterally and at the bottom, no brood	Thermoregulation, Resistance to mechanical perturbations	HEINRICH (1981c, 1981b, 1981a), CULLY & SEELEY (2004), PELEG & al. (2018), PETERS & al. (2022), SHISHKOV & al. (2022)
	Curtains	<i>A. dorsata</i> , <i>A. florea</i>	Nesting after emigration	(Queen pheromone)	Queen pheromone, Temperature, (Nasonov pheromone), (Tactile cues of comb)	Cluster of individuals, organised in hanging chains around a comb, contains brood	Thermoregulation, Nest defence, (Resistance to mechanical perturbations)	DYER & SEELEY (1991), KASTBERGER & STACHL (2003), JONES & al. (2007), KASTBERGER & al. (2011), THAPA (2011), BHAGAVAN & al. (2016), KASTBERGER & al. (2016)
Cover gaps	Plugs	<i>E. hamatum</i> , <i>E. burchellii</i>	Horizontal gap	Difficulty to walk	Stretching, Tactile stimulation	One to three ants cover a small pothole on the ground	Foraging efficiency	POWELL AND FRANKS (2007), HANAMOTO & MATSUNO (2011)
	Bridges	<i>E. hamatum</i> , <i>E. burchellii</i>	Horizontal gap	Difficulty to walk	Stretching, Tactile stimulation	Chain of ants covering large gap along the trail	Foraging efficiency	GARNIER & al. (2013), REID & al. (2015), GRAHAM & al. (2017), MCCREERY & al. (2022)
		<i>Oecophylla</i> spp.		Difficulty to walk + visual stimulus	(Stretching), Visual stimuli		(Foraging efficiency)	HÖLDOBLER & WILSON (1977)
	Hanging chains	<i>E. hamatum</i> , <i>E. burchellii</i>	Vertical gap	Difficulty to walk	(Stretching), (Tactile stimulation), (Load sustained)		(Foraging efficiency)	No study to date. Reported in KRONAUER (2020)
		<i>Oecophylla</i> spp.		Difficulty to walk + visual stimulus	Visual stimuli, Tactile stimulation, Chain size, (Stretching), (Load sustained)		(Foraging efficiency)	LIONI & al. (2001), LIONI & DENEUBOURG (2004), Carlesso & al. (in press)
	Scaffolding	<i>E. burchellii</i>	Inclined surface	Difficulty to walk	Slipping, (Tactile stimulation)	Clusters of ants gripping the substrate over an incline along the trail	Foraging efficiency	LUTZ & al. (2021)

Function	Structure	Species	Environm. context	Trigger	Individual-level stimulation	Description	Functional adaptations	References
Collective transport	Pulling chains	<i>L. cyanica-tena</i>	Predation	(Pulling nestmate + no movement)	(Feedback from prey item)	Chains of ants pulling prey	(Pulling force), (Coordination)	PEETERS & DE GREEF (2015), MIZUNO & al. (2022)
Nest building	Festoons	<i>A. mellifera</i> , <i>A. cerana</i>	Empty space within cavity	(Queen pheromone), (Empty space)	Clustering, (Temperature)	Cluster of bees organized in chains	Heat generation	No specific studies on festoons. Mentioned in: DARCHEN (1962), HEPBURN (1986), HEPBURN & MULLER (1988), MULLER & HEPBURN (1992), PRATT (1998), YANG & al. (2010), SMITH & al. (2017)
	Pulling chains	<i>Oecophylla</i> spp.	Leaf bending	Increased interaction rate, Nestmate pulling + no movement	Clustering, Feedback from substrate	Chains of ants pulling substrate	(Pulling force)	BOCHYNEK & ROBSON (2014)
Defence	Balling	<i>A. mellifera</i> , <i>A. cerana</i> , <i>A. adreniformes</i> , <i>A. dorsata</i>	Predatory threat	Hornet marking scent, Visual stimulus, Alarm pheromone	Visual stimulus, Hornet marking scent, Alarm pheromone	Cluster of non-connected bees surrounding predator	Heat generation, Asphyxiation	ONO & al. (1987), ONO & al. (1995), KEN & al. (2005), ABROL (2006), PAPACHRISTOFOROU & al. (2007), SUGAHARA & SAKAMOTO (2009), BARACCHI & al. (2010), SUGAHARA & al. (2012), TAN & al. (2016), HOSONO & al. (2017)
Survival	Rafts	<i>S. invicta</i> , <i>F. selysi</i>	Nest flooding	Water contact	Water contact, Tactile stimulation, Load sustained	~2.5 layers of workers on top of a layer of brood, enveloping the queen(s)	Waterproofing, Buoyancy, Resistance to mechanical perturbations	ADAMS & al. (2011), MLOT & al. (2011), MLOT & al. (2012), FOSTER & al. (2014), WAGNER & al. (2021)

and therefore does not trigger the morphological change of the aggregation. Indeed, vertical shaking can even lead to the structural failure of the cluster if the magnitude of the force applied is large enough.

Research on the mechanical adaptations of self-assemblages is still limited, but we hypothesise that structures sharing functionality and architectural features may show similar responses to perturbations. The bee curtains of *Apis dorsata* (Fig. 3B) and *Apis florea* (KASTBERGER & al. 2011, HEPBURN & al. 2014), the swarm clusters of *Apis mellifera* (Fig. 3A) (HEINRICH 1981b, SHISHKOV & al. 2022), and the bivouacs of *Eciton* army ants (Fig. 1A) (SCHNEIRLA & al. 1954) share several architectural features and are likely to be exposed to comparable environmental stressors. Comparing the functional adaptations of these structures may reveal shared behavioural mechanisms across species, shedding light on the evolution of self-assembly behaviour in insect societies.

**Water / raining conditions:** Rainfalls may threaten the integrity of self-assemblages by adding weight to the structure, by causing ruptures in the connections among individuals, or by cooling off the microenvironment within the structure and making thermoregulation more difficult. Protection from rain may be obtained by selecting repaired nest sites, as may be the case for *Eciton* army

ants' bivouacs (Fig. 1A) (SCHNEIRLA & al. 1954), or by waterproofing the surface of the self-assemblage. Water repellency may emerge as a passive property of the connectivity among neighbours or may be achieved through active behavioural responses to the sensation of water. The former case is found in the rafts and towers of *Solenopsis* fire ants, which show increased waterproofing compared with isolated individuals (Fig. 4A, C) (MLOT & al. 2011, PHONEKEO & al. 2017). Passive hydrophobicity, which may be induced by tiny hairs on the insect's cuticle (ADAMS & al. 2011, HURCHALLA & DRELICH 2019) or by their cuticular hydrocarbons (MENZEL & al. 2019, BLOMQUIST & GINZEL 2021), is likely to prevent colonies from sinking into water during the heavy floodings typical of their habitat (TSCHINKEL 2013). In addition, *Apis* bees actively increase the hydrophobicity of swarm clusters by forming a protective curtain in the outer layer of the structure (CULLY & SEELEY 2004, THAPA 2011). The response of bees to contact with water is stereotypical: Individuals positioned in the outer layer of the cluster increase their vertical alignment with neighbours, tuck their head beneath the wings of the bee directly on top, and hold their wings together. Curtains are transient properties of clusters, rapidly disappearing upon water evaporation, but allow bees to effectively shed most of the water falling on the structure (CULLY & SEELEY

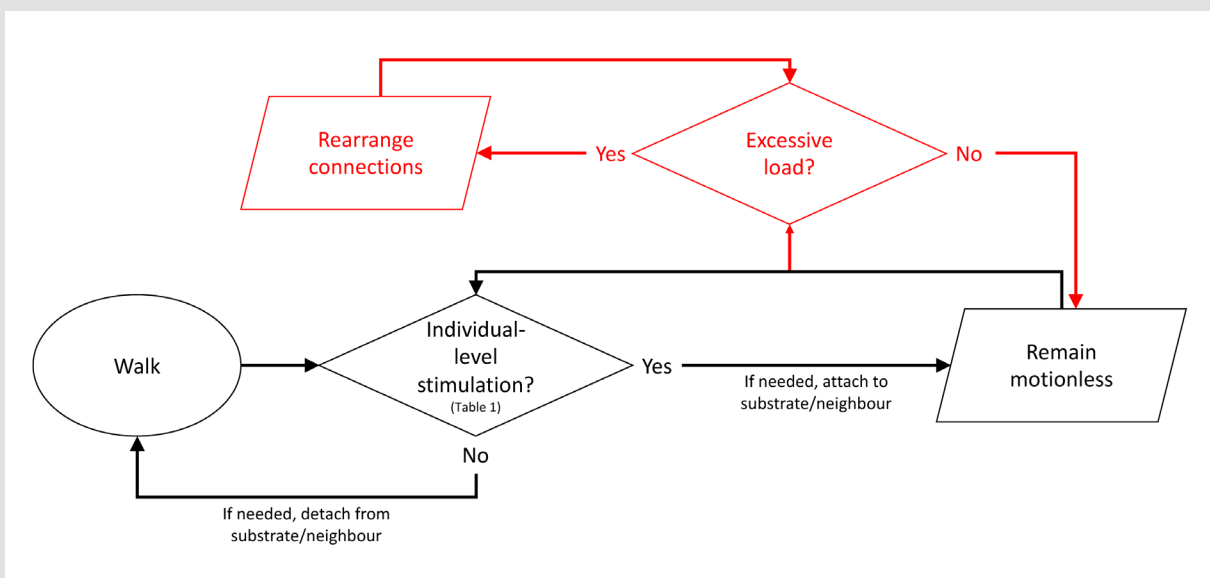


### Box 1: One rule to build them all?

Understanding the behavioural rules that insects use when self-assembling can provide researchers with important insights into the evolutionary path of self-assemblages. Looking at the data presented in Table 1, it is clear that some species have adapted their ability to self-assemble to perform multiple activities. It is possible that these species evolved self-assembly to solve a specific challenge in their habitat (i.e., gap crossing) and successively generalised these behavioural rules to other contexts (i.e., pulling chains for nesting). Alternatively, these species may be confronted with similar constraints in different contexts and thus evolved a common mechanism (self-assembly) for solving them (ANDERSON & al. 2002). Here, we use a simple flow chart to propose a simplified algorithm for self-assembly behaviour in the two social insect genera for which we have the most individual-level data – *Eciton* (army ants) and *Solenopsis* (fire ants). Our algorithm, while necessarily a simplification of the behaviour shown by ants, aims at providing researchers with a foundation upon which more complex rules can be built. Further, this algorithm can be extended to other social insect species once more is known about the proximate rules they use when self-assembling.

The flow chart shown below (Box 1 Fig.) illustrates the fundamental decision-making processes that an ant faces when self-assembling. The colour of the chart represents the ant species which the processes are applicable to: processes that apply to both genera are coloured black, whereas those illustrated in red only apply to *Solenopsis* ants. We suppose that an ant is walking, motivated by food or other relevant stimuli. The first decision-making step is determined by the detection of an environmental and / or social stimulus, listed in the column “Individual-level stimulation” of Table 1. The presence of this stimulus triggers the ant to remain motionless for a longer or shorter amount of time, during which she remains responsive to other stimulations. The continuous presence of the initial or other stimulation (i.e., tactile stimulation in *Eciton* and *Solenopsis* ants) inhibits the movement of the ant, thereby locking it in place for as long as needed. At this point, *Solenopsis* ants can perceive the load they carry and decide to rearrange their connectivity if this load becomes excessive (TENNENBAUM & al. 2016, PHONEKEO & al. 2017, VERNEREY & al. 2018). As soon as stimulation ends, the ant restores walking and the process restarts. These simple rules and their interactions seem sufficient for forming a range of structures (pothole plugs, bridges, chains, scaffolds, bivouacs, rafts, and towers), with the necessary structure emerging in the appropriate environmental context.

In its current version, our flow chart assumes that insects within the colony are identical to each other and that their responses towards stimuli are hard-wired. However, individuals within social insect colonies are not identical to each other: they may differ in sensory threshold (SCHEINER & al. 2004), morphology (POWELL & FRANKS 2006), genetics (OLDROYD & FEWELL 2007), nutritional status (MAILLEUX & al. 2010), and / or experience (RAVARY & al. 2007, ARENAS & al. 2009). These differences cause individuals to respond differently to the same



**Box 1 Fig.:** Flow chart showing a simplified individual-level algorithm for self-assembly formation in *Eciton* army ants and *Solenopsis* fire ants. The chart is built on our current knowledge of the proximate mechanisms governing the emergence of self-assemblages in these two genera. Parts coloured in red are mechanisms only known in *Solenopsis* ants. Oval represents the starting point, parallelograms indicate behavioural output, diamonds indicate decisions.

stimulation, and have thus the potential to impact self-assembly formation (see “The role of inter-individual heterogeneity” section). Our flow chart can be simply extended to represent inter-individual heterogeneity by assigning probabilities to each step that may differ for each individual. Some ants may be more likely to perceive a trigger stimulus due to their caste, role, or position, and may in turn “seed” the emergence of a self-assembly. For instance, motivational factors may allow ants to persist more in a behaviour – that is, remain motionless for a longer period of time when not inhibited by tactile cues – and thus facilitate the maintenance of the structure. Larger ants may be able to sustain heavier loads while in a structure, strengthening its architecture and decreasing the likelihood of failure. Variability among individuals is a likely way in which natural selection may act upon colony-level traits (JEANSON & WEIDENMÜLLER 2014), and this includes self-assembly. Implementing variability in models of self-assembly will deepen our knowledge of its role in self-organisation and provide powerful insights into the mechanisms of natural selection in collective behaviour.

Our chart lends itself well to validation through behavioural experiments and computational modelling. While the chart was created based on the current knowledge of the behavioural rules that *Eciton* and *Solenopsis* ants use when self-assembling, it also provides a guide for testing each decision-making step in isolation. For instance, it is well-established that tactile stimulation inhibits the movement of *Eciton* army ants that participate in plugs and bridges (POWELL & FRANKS 2007, GARNIER & al. 2013). This mechanism has been derived by detailed analyses of the behaviour of ants in structures but never verified in isolation. One may validate this behavioural rule by isolating individuals forming plugs and provide artificial tactile stimulation with a brush or similar object. This would also allow researchers to precisely identify which stimulation is necessary to inhibit ants’ motion (i.e., is tactile stimulation enough by itself, or are other signals exchanged as well?). Similarly, the shape of the rafts and towers formed by *Solenopsis* ants seems to be limited by the weight that each individual can sustain before rearranging its connectivity with neighbours (MLOT & al. 2011, TENNENBAUM & al. 2016, PHONEKEO & al. 2017, VERNEREY & al. 2018). The description of this rule, however, originates from a combination of behavioural studies on the whole structure and rheology testing but never empirically verified. This hypothesis may be experimentally tested, for instance, by artificially increasing the weight on ants through magnetic paint, which can then be even further manipulated by placing a magnet at variable distances from the structure. Our chart also provides a baseline algorithm as a starting point for developing computational models of self-assembly behaviour. Although very simplistic, the aim of the chart is to show that insects may not need to possess a separate set of behavioural rules for each structure. Algorithms of self-assembly behaviour have so far been developed for solving a specific challenge and rarely tested in a variety of contexts (OZKAN-AYDIN & GOLDMAN 2021, GARDI & al. 2022). Computer scientists can refer to the proposed chart for drawing ideas from social insects’ self-assembly behaviour to develop algorithms that allow multi-agent systems to respond adequately to the needs of the group depending on the surrounding context (SAHIN & al. 2002, MALLEY & al. 2020, SWISSLER & RUBENSTEIN 2020).

2004). Similar rain shedding behaviour is observed in the open-nesting dwarf bees *Apis florea* and *Apis andreniformis* (see THAPA 2011), and it is likely to be widespread among bee species that form bee clusters. Curtain formation is a stark example of how small, local adjustments made by individual insects within the structure can lead to large functional adaptations of the assemblage as a whole, minimising the impact of external stressors and enhancing the colony’s survival probabilities.

**Temperature:** Many social insects keep their nest temperature within narrow ranges to ensure optimal brood development and maintain adequate workers’ activity levels (JONES & OLDROYD 2006). Self-assemblages that house colonies for extended periods of time need to be thermoregulated to minimise the impact of diel temperature fluctuations and thermal extremes on the insects. Thermoregulation has so far been described only in the bivouacs formed by *Eciton* army ants (Fig. 1A) (FRANKS 1989, BAUDIER & al. 2019, BAUDIER & PAVLIC 2022) and the swarm clusters (Fig. 3A) (HEINRICH 1981a, OCKO & MAHADEVAN 2014, PETERS & al. 2022) and bee curtains of *Apis*

bees (Fig. 3B) (DYER & SEELEY 1991, MARDAN & KEVAN 2002, JONES & al. 2007, KASTBERGER & al. 2016). The micro-climate of these assemblages is regulated through passive and active mechanisms (JONES & OLDROYD 2006). Adequate nest site selection allows colonies to settle in favourable thermal environments and reduce the energy that workers need to spend on active cooling or heating behaviours. For instance, colonies of the army ant *Eciton burchellii parvispinum* select subterranean bivouacking sites when in hot arid environments. These sites are cooler than the surrounding environment and protect ants from temperature peaks through the day (BAUDIER & al. 2019). Ants, however, prefer warmer-than-environment nesting sites at higher altitudes where ambient temperature is lower. Self-assemblages also show partial changes in their morphology in response to sudden exposure to external stressors. Army ants’ bivouacs change their shape when partially exposed to sunlight, as exposed ants quickly leave their positions and move towards shaded sections of the structure (SCHNEIRLA & al. 1954). Persistent perturbations can even cause the dismantling of the bivouac and the

relocation of the colony (SCHNEIRLA 1971). Similarly, *Apis florea* bees build their nests in shaded areas and rapidly migrate if they become exposed to sun for prolonged periods of time (SEELEY & al. 1982, DEOWANISH & al. 2001). Insects can strategise their exposure to environmental factors by regulating the orientation of their nests. For instance, the open-nesting bees *Apis dorsata* and *Apis laboriosa* orientate their nests in a southerly direction to maximise sun exposure during the day and favour the early onset of foraging (UNDERWOOD 1990, OLDROYD & WONGSIRI 2009).

The micro-climate of self-assemblages can be further regulated through the active engagement of individuals in cooling or heating behaviours (JONES & OLDROYD 2006). Strikingly, many thermoregulatory strategies are shared across structures. Self-assemblages show profound morphological changes in relation to the external ambient temperature, contracting in cold weather and expanding as temperature increases (HEINRICH 1981b, FRANKS 1989, DYER & SEELEY 1991, PETERS & al. 2022). These changes emerge from the inter-individual spacing preferences of insects within the structure: Individuals pack densely together when ambient temperature is low, thereby minimising the surface area of the structure exposed to the external environment and insulating the warm core of the aggregation; in hot weather insects increase their spacing, creating empty spaces within the aggregation and facilitating air convection and thus cooling. Changes in ambient temperature are perceived by workers in the outer layers of the clusters, whose behaviour – either distancing or packing together – broadcasts information to the internal layers of the structure (HEINRICH 1981b, OCKO & MAHADEVAN 2014). In honey bees, high temperature triggers individuals to move from the warm core of the swarm cluster towards the cooler outer layers. The continuous outward motion of individuals contributes to the formation of empty tunnels across the structure that further facilitate air circulation and heat loss (HEINRICH 1981c). Tunnels have also been observed in the bivouacs of *Eciton* army ants (FRANKS 1989, BAUDIER & PAVLIC 2022), which are most likely used by ants to feed brood items stored within the structure. These tunnels may help colonies to cool down the structure in hot environments. Although ants are not able to fan for obvious reasons, the simple motion of individuals from warm regions of the structure to cooler ones may be sufficient to shed heat and reach homeostasis (BAUDIER & PAVLIC 2022). Recent studies using CT scanning on swarms (Fig. 3A) and bivouacs (Fig. 1A) are promising avenues for shedding light on the internal dynamics of these structures (BOCHYNEK & al. 2021, SHISHKOV & al. 2022). Insects can regulate the temperature of self-assemblages by adjusting their collective metabolic heat (HEINRICH 1981a, b, WEIDENMÜLLER 2004, BAUDIER & al. 2019). Honey bees are known to engage in fanning or shivering behaviours in response to high and low temperatures, respectively (HEINRICH 1981b). Increased metabolic heat has also been found in *Eciton* army ants exposed to low temperatures (BAUDIER

& al. 2019), but the behavioural mechanisms underlying this process are still unclear.

Bees of the genus *Apis* also self-assemble to generate heat for activities other than nest thermoregulation. When occupying a new nest site, bees group into festoons (Fig. 3C) – clusters of individuals organized in chains and linked to each other through leg attachments – to initiate comb building (HEPBURN 1986, ANDERSON & al. 2002, YANG & al. 2010, SMITH & al. 2017). Temperatures within festoons are generally five or more degrees higher than in the surrounding empty space (HEPBURN & MULLER 1988), thereby creating a thermal microenvironment that facilitates wax manipulation and deposition. Festoons are composed of a specialised cohort of “builders” (MULLER & HEPBURN 1992, PRATT 1998) and may function as blueprints for comb positioning within the hive (DARCHEN 1962). Future studies should test the functionality and flexibility of these structures and describe the behavioural mechanisms that lead to their formation in hives. Heat production has also been proposed as the mechanism underlying the anti-predatory “balling” behaviour exhibited by several species of *Apis* bees (Fig. 3D) (ONO & al. 1987, 1995, KASTBERGER & STACHL 2003, BARACCHI & al. 2010). Balling consists of groups of bees – usually between 30 and 300, depending on the attacker’s size (TAN & al. 2016) – rapidly engulfing an attacker and killing it by increasing the internal temperature of the cluster by activating their wing muscles (KEN & al. 2005, ABROL 2006, SUGAHARA & SAKAMOTO 2009, HOSONO & al. 2017). Attacking bees link to each other via leg connections and produce temperatures up to 45.6 °C, which is higher than the thermal lethal limit of hornets but lower than their own (ONO & al. 1987, 1995). The cluster disassembles only once the predator is killed. Balling behaviour is likely initiated by few individuals detecting the predator visually (KEN & al. 2005) or chemically (ONO & al. 1995) and then promoted by the emission of alarm pheromone by attacking bees (TAN & al. 2016). However, it remains unclear whether the attacker is actually killed by the heat generated by bees or by other concurrent factors. Heat seems to be the primary cause of death for *Vespa mandarinia japonica* wasps attacked by *Apis cerana* (see ONO & al. 1987, 1995), two species sharing a long co-adaptation history (FUCHS & TAUTZ 2011). In other bee species, the increased humidity and CO<sub>2</sub> concentrations inside the clusters, and possibly stinging behaviour, are likely to be critical for killing the engulfed opponent (PAPACHRISTOFOROU & al. 2007, SUGAHARA & SAKAMOTO 2009, SUGAHARA & al. 2012).

### Weight as structure shaper

Weight distribution is a major factor for the growth of self-assemblages. Equal load share among insects protects self-assemblages against the risk of individual failure and prevents the maximum growth of the structure from being limited by the strength of individual insects. It also prevents individual insects from being overloaded, which may pose a risk to the structural integrity of the self-assemblage and lead to catastrophic consequences for the colony.

The formation process of the structure determines how weight is distributed among individuals, whereas the final shape of the structure is likely to be constrained by the maximum load that individuals are able to carry. For example, *Solenopsis* fire ants carry loads of ~3 ant-body weights while participating in towers, but only ~1.5 ant-body weights when in rafts (MLOT & al. 2011, PHONEKEO & al. 2017). The formation process of rafts and towers explains the difference in the load sustained by ants. Rafts are flat aggregations that reach an equilibrium at  $\sim 2.5 \pm 0.4$  layers of ants, where the bottom layer of ants in contact with water is kept motionless by the nestmates walking on top of them (MLOT & al. 2011). The load of ~1.5 ant-body weights is minimal because thinner rafts would not be cohesive as the number of freely-moving individuals walking on top of the structure would not be sufficient to keep structural individuals motionless. Towers, however, start as flat aggregations that grow in height around vertical supports (PHONEKEO & al. 2017). As ants start climbing on top of each other, individuals within the aggregation sustain their maximum load capacity, and only stable portions of the structure can form while unstable portions collapse. The load of ~3 ant-body weights is maximal, and the growth of the tower is limited by the maximum load capacity of ants. Weight distribution in other self-assemblages is still poorly understood. Recent work indicates that honey bees' swarm clusters are organised so that each layer of bees supports a weight that scales with its mass to the ~1.5 power (SHISHKOV & al. 2022). The arrangement of bees within the cluster ensures that each layer utilises an equal fraction (1/3) of its maximum strength. The weight sustained by each bee depends on her positioning within the cluster. Bees closer to the attachment point of the cluster sustain maximum loads of 3.8 bee-body weights, while bees at the tip of the cluster sustain minimal loads. Similarly, *Eciton* army ants participating in bivouacs share similar loads among them (BOCHYNEK & al. 2021).

Insects can actively regulate the load they carry to avoid injuries or excessive loads while participating in self-assemblages. Extensive work on fire ants' aggregations revealed that ants continuously rearrange their leg connections with neighbouring individuals to redistribute local strains (TENNENBAUM & al. 2016, TENNENBAUM & FERNANDEZ-NIEVES 2017, VERNEREY & al. 2018, TENNENBAUM & FERNANDEZ-NIEVES 2020). Ants perceiving loads higher than ~3 ant-body weights release their legs and play dead. The value of ~3 ant-body weights carried by ants while in towers (PHONEKEO & al. 2017) is much lower than the weight a free ant can sustain without being injured (~750 ant-body weights, or 0.8g) (MLOT & al. 2011, FOSTER & al. 2014, TENNENBAUM & al. 2016), but it is consistent with the force needed to overcome the friction of their leg joints – that is, the energy required for passively detaching the ant's leg from a neighbour (TENNENBAUM & al. 2016). This suggests that the threshold that triggers ants to regulate their behaviour is determined by the strength of the connections among neighbours

rather than by the maximum strength of ants (FOSTER & al. 2014, TENNENBAUM & al. 2016). More research is needed to determine whether similar behavioural rules can be found in other species, such as *Eciton* army ants or *Apis* bees. Bees participating in swarm clusters carry a maximum load of 3.8 bee-body weights, independently from cluster size, despite single individuals being able to sustain loads of  $35 \pm 14$  bee-body weights (SHISHKOV & al. 2022). *Eciton* ants in bivouacs carry maximum loads of 12 ant-body weights (BOCHYNEK & al. 2021), which is likely to be much lower than their maximum load capability. The ability to rearrange the internal network of connections is likely to be facilitated or constrained by the biomechanics of these connections. Fire ants predominantly connect with their neighbours using adhesive pads connected to a neighbour's tarsus (FOSTER & al. 2014), which can be easily detached when in need (FEDERLE & al. 2002). By contrast, *Eciton* army ants exclusively interlock their well-developed tarsal claws with those of their neighbours, a connection which may be more difficult to break. Different types of attachments may limit the mobility of individuals within the aggregation and hinder their ability to redistribute loads. Recent research on *Apis* swarm clusters revealed that bees adjust the length of a cluster more rapidly than its diameter, suggesting that mechanical constraints may limit the ability of bees to re-distribute the weight of the structure among them (SHISHKOV & al. 2022).

## Understudied aspects of self-assembly

### Environmental geometry

The geometry of the environment defines the space in which insects interact and profoundly shapes the emergence of collective patterns (PINTER-WOLLMAN & al. 2017). The initiation of self-assembly is often triggered by environmental features that limit the movement of individuals, which increase aggregation and in turn the frequency of inter-individual interaction among group members. In fact, any stimulus that increases the density of individuals in a limited space facilitates self-assembly formation (ANDERSON & al. 2002). This mechanism seems to be shared across species that form self-assemblages. *Solenopsis* fire ants join rafts and towers when encountering empty spaces on the surface of the structure and decide to remain in place depending on social information (MLOT & al. 2011, PHONEKEO & al. 2017, WAGNER & al. 2021). The pulling chains formed by *Oecophylla* ants (Fig. 2A) during nest building are more likely to be initiated at the tip of leaves, where the reduced surface area of the leaf tip slows ants down and increases their interaction rates (BOCHYNEK & ROBSON 2014). All the self-assemblages built by foraging *Eciton* army ants (Fig. 1B, C, D) are initiated in response to environmental obstacles obstructing the movement of ants (POWELL & FRANKS 2007, REID & al. 2015, LUTZ & al. 2021, MCCREERY & al. 2022). Ants encountering potholes along the ground are forced to slow down and extend over it, where they can decide to plug the hole or keep walking depending on tactile cues (POWELL & FRANKS

### **Self-assembly within species – same rules, different structures?**

Research investigating the behavioural rules followed by social insects when self-assembling has so far focused on individual structures. However, whether insects follow similar rules when self-assembling into different structures has been seldom explored. PHONEKEO & al. (2017) and NAVE & al. (2020) showed that the behavioural rules that underlie raft formation in *Solenopsis* ants can be successfully used to simulate tower formation in the same species of ant. Is this the case in other species as well?

### **Self-assembly between species – different rules, same structure?**

While the behavioural rules followed by a certain species may be similar across structures, similar self-assemblages may emerge from different behavioural algorithms when formed by different species. For instance, *Oecophylla* and *Eciton* army ants build bridges when covering horizontal gaps encountered along trails. The local rules and stimuli used by each species when self-assembling are determined by their ecological context. Behavioural algorithms that converge into similar final outcomes (i.e., bridges) may have different intermediate states. Whether one algorithm is favoured over another may then be determined by the specific ecological pressures faced by each species. Future research should compare the behavioural algorithms used by species forming comparable self-assemblages and focus not only on the final state of the structure but also on the intermediate stages that lead to its formation.

### **Heterogeneity within the group**

Most of the studies modelling self-assembling behaviour have assumed all individuals in a group to be identical to each other. However, research on other forms of collective behaviour has shown that inter-individual heterogeneity within groups can greatly enhance the performance of the group. Many self-assemblages are formed by individuals varying in their physiology and morphology. How does this heterogeneity effect the functionality of self-assemblages?

### **Geometrical features of the environment**

The geometry of the environment where a self-assemblage is formed is likely to have a profound impact on the functionality of the structure. For instance, *Eciton* ants optimise the shortcuts they form using bridges according to the angle of the intersection they cover. The shape of a self-assemblage is likely to impact the information flow among structural individuals, which may receive different signals depending on the position they occupy within the structure. Future research should investigate the impact that environmental geometry has on the functionality of self-assemblages.

### **Architecture of self-assemblages**

Technological limitations have so far prevented scientists from investigating the internal architecture of self-assemblages without disrupting the structure. The availability of new tools such as portable X-ray- and CT-scanners has recently allowed unprecedented imaging of the internal skeleton of *Eciton* ants' bivouacs and *Apis* bees' swarm clusters without disruption. These technologies will allow scientists to accurately investigate the internal architecture of self-assemblages and how this is affected by the outer shape of the structure or other exogenous factors (i.e., temperature). Understanding the architecture of self-assemblages will provide important insights on the constraints which insects within structures are subject to and on the functional limitations of the assemblages themselves.

### **Between-colony variation**

Research on self-assembly has to date investigated the behavioural algorithms that underlie the emergence of structures in one species or another. Colonies, however, have been shown to vary in several traits, including collective behaviour. The likelihood of forming self-assemblages or the way that a self-assemblage is formed in a specific context may vary among colonies. Given the inter-group variation found in other forms of collective behaviour, studying whether, how, and why social insect colonies vary in self-assembly behaviour is a promising avenue of research.

### **Evolution of behavioural algorithms for self-assembly**

Virtually nothing is known about the evolution of self-assembly behaviour in social insects. As for any other phenotypic trait, ecological pressures likely shaped the behavioural algorithms that insects use when self-

assembling. In turn, over evolutionary timescales, the ability to form structures has likely shaped the sensory abilities and rules that insects use to self-assemble – for instance, refining the “refractory” time that *Eciton* ants spend motionless after sensing tactile stimulation to make bridges stable in spite of traffic fluctuations. Studying the evolution of self-assembly will shed light on how the ecological pressures faced by each species have shaped the interaction rules used when self-assembling.

2007, GARNIER & al. 2013). The same behaviour underlies bridge formation: Ants initiate bridges where the gap can be easily covered by a single individual, and only subsequently the structure is moved to span a larger distance (REID & al. 2015, GRAHAM & al. 2017). Ants passing over bridges may sense pothole-like gaps in the structure and decide to join it only if walked over by nestmates (POWELL & FRANKS 2007). Similarly, the formation of scaffolds is triggered by ants slipping while crossing an inclined surface (LUTZ & al. 2021). Even though other local cues influence ants’ decisions to participate in self-assembly (LIONI & al. 2001, LIONI & DENEUBOURG 2004, MCCREERY & al. 2022), these studies suggest that the presence of environmental features that impede the movement of ants play a central role in the initiation of building behaviour (particularly when the purpose of the structure to be built is explicitly to facilitate traffic flow, as in *Eciton* bridges). An obvious exception is that of honey bees, whose flight abilities prevent them from getting stuck in obstacles along the terrain. The aggregation process in bees is mediated by the emission of pheromones (VANDER MEER & al. 1998, BARACCHI & al. 2010, PIRK & al. 2011, TAN & al. 2016, NGUYEN & al. 2021), which plays a key role in coordinating the movement of individuals around relevant targets (see “Pheromones” section).

Environmental geometry plays a primary role in determining the final shape of the self-assemblages. For instance, the extent of the movement of *Eciton* ants’ bridges across a gap depends on the angle at which two trails diverge from each other (REID & al. 2015, GRAHAM & al. 2017). The morphology of bivouacs largely depends on the geometry of the nesting site selected by ants (SCHNEIRLA & al. 1954): Bivouacs are most frequently cylindrical, but they may resemble a “curtain” when the nesting site only has a partial wall, or a “pouch” when the supporting surface is far from the ground. Similarly, *Apis* bees’ swarm clusters adapt to the shape of the branch they choose as a support. The geometry of nest cavities may also influence the formation of festoons by *Apis* bees when occupying new nest sites, potentially determining where combs will be built (DARCHEN 1962, SMITH & al. 2017). Understanding the mechanisms that underlie the adaptations of self-assemblages to the surrounding environmental geometry will shed light on the local stimuli that govern the decision-making processes and communication among individuals within structures.

Self-assemblage morphology has the potential to modify the communication among individual insects or the information they receive, in turn affecting the way insects

react to environmental stimuli. Army ants’ bivouacs and bees’ swarm clusters can incorporate tree branches in the assemblage when necessary (Figs. 1A; 3A) (SCHNEIRLA & al. 1954), which may provide additional support to structural insects. Environmental perturbations such as wind may thus differentially affect sections of the structure and cause modular changes in its morphology – for example, swarm clusters incorporating an additional branch may respond to horizontal oscillations by spreading out in some sections but not in others (PELEG & al. 2018). Modular responses in other self-assemblages occur as insects occupying different sections of the structure receive different local information. This is observed in the bridges formed by *Eciton* army ants (as described in “Tactile stimulation” section), where differences in the traffic flow between the inner and outer edge of the structure causes bridges to move across a gap (REID & al. 2015, GRAHAM & al. 2017). Research investigating the links between the morphology of self-assemblages and their functional responses to perturbations will deepen our knowledge on how information is integrated in the aggregation and will lead to the development of models that can mimic the functionality of these structures in naturalistic conditions.

Self-assemblages are systems in which the interactions among individuals have the potential to cause an instantaneous change in the geometrical space in which these interactions occur. This opens up unique opportunities for studying the interactions between individuals and their environment and how this information transfer shapes the emergence of collective behaviour. An example is that of the hanging chains built by *Oecophylla* ants when bridging vertical gaps encountered along their foraging trails (Fig. 2C) (LIONI & al. 2001, LIONI & DENEUBOURG 2004). As a chain grows, the individual-level probability for ants to join the structure increases while that of leaving it decreases. This mechanism allows ants to focus their efforts on the formation of a single chain instead of multiple unsuccessful ones (LIONI & DENEUBOURG 2004), and it may be mediated by the presence of visual stimuli in the environment (HÖLLDOBLER & WILSON 1977, CARLESSO & al. in press) or by the number of ants already in the chain (LIONI & al. 2001, LIONI & DENEUBOURG 2004). The movement of rafting fire ants is necessarily limited by the surface area of the structure (MLOT & al. 2011, 2012). Small heterogeneities along the perimeter of the raft lead to the emergence of finger-like protrusions growing from the structures’ edge (WAGNER & al. 2021), which ants can use to explore the surrounding environment and reach shore. The growth of protrusions is promoted by the clustering

of individuals along edge inconsistencies, which increases the frequency of interaction among nestmates and in turn their deposition rate in these areas. This generates a positive feedback loop as the protrusions cause more clustering and promote their own growth. Similar dynamics may underlie the formation of bridges in the same species of ants (EGAN & al. 2022). Interestingly, the phenomenon is nearly identical to the dynamics underlying tunnel excavation in nesting ants (BUHL & al. 2005), where digging rates are modulated by the interplay between tunnel geometry and density of ants.

### **The role of inter-individual heterogeneity**

Collective behaviour research has mostly focused on discovering universal mechanisms underlying the emergence of group-level patterns, often reducing all group members to identical units and neglecting any inter-individual variability (CAMAZINE & al. 2001, JOLLES & al. 2020). Individuals within colonies are, however, not identical to each other. Aside from the reproductive division of labour between queen and workers, individuals may differ in morphology, age, nutritional state, experience, or other phenotypical or behavioural traits (JEANSON & WEIDENMÜLLER 2014). This variability affects the way each insect perceives and responds to external stimuli and in turn the collective behaviour of the group (JOLLES & al. 2020, WALSH & al. 2021). In this section, we review the current knowledge on the role of individual variation in self-assembly behaviour and highlight promising future directions for understanding the impact of heterogeneity on the structural and functional properties of self-assemblages.

The position that an individual occupies in a self-assemblage may be determined by its physiological, morphological, or reproductive characteristics. This moderates which group members are exposed to the elements and other environmental perturbations and which are instead well-protected within the structure. Queens – the most important members of a colony – are always found at the core of the aggregations, where they benefit from the thermoregulation and extra protection offered by the surrounding layers of workers (SCHNEIRLA & al. 1954, HEINRICH 1981b, ADAMS & al. 2011, PURCELL & al. 2014). For example, the queen and brood items are kept within empty chambers at the core of *Eciton* army ants' bivouacs (SCHNEIRLA & al. 1954, BOCHYNEK & al. 2021). Brood items are organised concentrically from the core of the structure to its outer layers, with smaller larvae kept at the centre and larger ones at the periphery (SCHNEIRLA & al. 1954). SCHNEIRLA (1971) reported that small workers are more likely to occupy the inner regions of the bivouac, whereas the outer layers of the structure are mainly composed of large workers. Although this needs to be quantified rigorously, this composition may decrease the overall mortality of colony members as large workers are more thermally resistant and less prone to desiccation than their smaller nestmates (SCHNEIRLA & al. 1954, SCHNEIRLA 1971). At the proximate level, this distribution may be driven by the

physiological needs of individuals – with smaller workers seeking the warmest areas of the structure – or by division of labour if minor workers dedicate themselves to brood care within the inner layers of the bivouac. Similarly, the distribution of workers in the swarm clusters and protective curtains formed by *Apis* bees is organised by age (HEINRICH 1981a, SEELEY & al. 1982, CULLY & SEELEY 2004). Older workers compose the outer layer of the aggregations, while young colony members remain at the core of the clusters. The benefit for the colony is twofold. First, young bees have lower metabolic heat and are less capable of thermoregulation (HEINRICH 1981b, FAHRENHOLZ & al. 1989) and may thus gain more benefit from the warm micro-climate at the cluster's centre; second, given their larger residual lifespan, young bees represent an asset for the colony and remaining in the inner regions of the clusters may give them additional protection from environmental dangers (SEELEY & al. 1982). Young bees usually perform nest maintenance and brood care tasks (DYER & SEELEY 1991, BHAGAVAN & al. 2016, BHAGAVAN & BROCKMANN 2019), which may explain why they are under-represented in the curtains of open-nesting *Apis* species (SEELEY & al. 1982, DYER & SEELEY 1991).

The performance of self-assemblages can be enhanced by the morphological features of some group members. For example, brood items increase the buoyancy of the rafts built by *Solenopsis* fire ants (Fig. 4A) and *Formica selysi* ants (Fig. 4B) (ADAMS & al. 2011, PURCELL & al. 2014). In both species, brood items are kept at the bottom of the raft where they are in direct contact with water. This disposition emerges from the tendency of ants to form brood piles and aggregate on top of them in response to flooding. While the presence of brood is not critical to the functionality of a raft (ADAMS & al. 2011, PURCELL & al. 2014, AVRIL & al. 2016), the maximum rafting time of fire ants increased from an average of 12 hours when only workers were present to an average of  $7 \pm 3.24$  (mean  $\pm$  standard deviation) days (and up to 12 days) when larvae were incorporated into the structure (ADAMS & al. 2011). Brood items are more buoyant than workers (ADAMS & al. 2011, PURCELL & al. 2014) and help collect air bubbles underneath the raft (ADAMS & al. 2011). The buoyancy of the raft is further enhanced by the slightly hydrophobic cuticle of adult workers, which aids the trapping of air plastrons within the raft and decreases its material density (ADAMS & al. 2011, MLOT & al. 2011). The cuticle of *F. selysi* workers is covered in setae that may be effective in collecting air bubbles (SEIFERT 2002), but this needs to be confirmed by quantitative experiments. The disposition of workers within rafts is not casual either. In fire ants, workers are organised by size: Large workers compose the bulk of the structure, whereas smaller individuals fill the empty gaps between larger nestmates (FOSTER & al. 2014). This distribution strengthens the raft by increasing the connectivity within the aggregation, decreasing the likelihood of breakage caused by environmental perturbations (FOSTER & al. 2014, TENNENBAUM & al. 2016). AVRIL & al. (2016) demonstrated that workers of *F. selysi*

tend to occupy the same regions of the structure over consecutive raft formations. This consistency is likely to be caused by division of labour within the colony: Nurses may be responsible for piling brood items when water level increases, which would cause them to be more represented in the bottom and middle layers; on the other side, foragers may be the last individuals to join the structure and may thus be over-represented in the outer layers.

Some individuals may be more or less likely to participate in self-assembly behaviour due to their morphological or behavioural traits. In *Eciton* army ants, minor workers are more likely to be part of plugs and bridges compared with major and sub-major ants (POWELL & FRANKS 2007). This is due to the smaller body size of these workers: Small individuals are more likely to be hindered by potholes encountered along the terrain and be walked over by nestmates, which causes them to remain in the position of covering the hole. Since small workers are slower than their larger foraging-specialised nestmates, their specialisation in self-assembly has the added benefit of increasing the foraging efficiency of the colony by allowing other ants to attain their maximum speed (POWELL & FRANKS 2007, HANAMOTO & MATSUNO 2011). Although not yet tested, a similar mechanism may influence the joining decisions of *Solenopsis* fire ants when building rafts and towers (MLOT & al. 2011, FOSTER & al. 2014, PHONEKEO & al. 2017). Other factors may influence the likelihood of individuals to participate in self-assembly formation. Even small numbers of informed individuals have been shown to be able to guide groups towards nest sites or profitable food sources (COUZIN & al. 2005, SCHULTZ & al. 2008, DYER & al. 2009, GELBLUM & al. 2015). Some self-assemblages may benefit from the presence of leaders in the group. For instance, the hanging chains formed by *Oecophylla* ants (Fig. 2C) are guided by the presence of a visual stimulus (LIONI & al. 2001, LIONI & DENEUBOURG 2004, CARLESSO & al. in press). Associating a stimulus with the presence of a food source may increase the likelihood of observing the formation of chains, for instance, by increasing the time that informed individuals spend in the chain.

## Conclusions and future directions

The proximate mechanisms underlying self-assembly behaviour in social insects have long remained elusive due to inherent properties of these aggregations, which challenged many of the common methodologies available in the field of animal behaviour. In the last two decades, the increased accessibility to advanced technological tools and controlled laboratory conditions allowed scientists to deepen our understanding of the mechanisms governing the emergence of self-assemblages. This led not only to thorough descriptions of many of the local stimuli available to insects when self-assembling but also to the development of bioinspired solutions in swarm robotics (RUBENSTEIN & al. 2014) and material sciences (VERNERREY & al. 2019). The field of self-assembly behaviour in insect societies is more active than ever, with scientists

from several disciplines studying self-assemblages from different points of view (HU & al. 2016, VERNERREY & al. 2019). Future research will shed light on the full range and limitations of the adaptations that these structures can achieve as well as their evolutionary history. Recent work comparing self-assemblages with other morphogenesis processes at the molecular level has shown striking similarities (MURATORE & GARNIER 2023), highlighting the critical role that self-assembly plays at different biological scales and opening opportunities to generate new comparative research across biological levels.

Here, we reviewed the individual-level mechanisms that allow social insects to link their bodies together and form a coherent three-dimensional structure that spans several times the size of an individual. We also highlighted two understudied factors that have the potential to profoundly impact the morphological and functional adaptations of self-assemblages – environmental geometry and inter-individual heterogeneity. While several studies to date have shown how the environmental geometry has an impact on the final shape of self-assemblages (SCHNEIRLA & al. 1954, REID & al. 2015, PHONEKEO & al. 2017, LUTZ & al. 2021), only a handful of them have investigated the functional adaptations of these structures when subjected to dynamic environments (CULLY & SEELEY 2004, PELEG & al. 2018, MCCREERY & al. 2022, PETERS & al. 2022). Given the striking ability of self-assemblages to adapt to changes in local conditions (CULLY & SEELEY 2004, KRONAUER 2020), studying their functional adaptations to dynamic environments will help shed light on the local stimuli insects react to when perturbed and the time scale of their responses (PELEG & al. 2018). Further, self-assemblages are unique in that the interactions among individuals in the structure can instantaneously modify the environment in which these same interactions occur. This makes self-assemblages ideal model systems to investigate the feedback loops between individuals and the environment and how these shape future interactions (PINTER-WOLLMAN & al. 2017).

A second area seldom explored is the impact of group heterogeneity on the functionality and efficiency of self-assemblages. In social insect colonies, inter-individual variations in response thresholds and morphology are important variables for the functioning of the group (JEANSON & WEIDENMÜLLER 2014). Research exploring group composition in self-assemblages showed promising results (SCHNEIRLA & al. 1954, DYER & SEELEY 1991, POWELL & FRANKS 2007, GARNIER & al. 2013, PURCELL & al. 2014), suggesting that inter-individual variation may play a critical role in these structures. Colony rearing in laboratory conditions allows researchers to modify intra-group variability and study its effects on the functioning of the self-assemblages. Recently, manipulations of the phenotypic composition of social insect colonies have been used to study the consequences of heterogeneity on their collective behaviour (COOK & al. 2020, ULRICH & al. 2021). Future studies should investigate how intra-colony individual variation affects the functionality and efficiency



of self-assemblages, as recently investigated in other animal groups (JOLLES & al. 2020).

While research has unveiled the proximate mechanisms underlying self-assembly behaviour, there is still a paucity of information on its evolution within social insects. There are more than 15,000 ant species and 20,000 bee species in the world, yet only a handful of them have evolved the ability to self-assemble into functional structures. Among these, the picture is dominated by three genera – *Apis*, *Eciton*, and *Oecophylla* – which adapted self-assembly to accomplish multiple functions rather than just one (Tab. 1). These species may have evolved self-assembly behaviour to solve a particular challenge and then generalised this ability to other functions, or alternatively they may have been confronted with similar constraints in different contexts and thus evolved a common mechanism (self-assembly) for solving them (ANDERSON & al. 2002). Further, we still lack information about the proximate mechanisms of self-assembly in other species. For instance, *Leptogenys cyanocatena* is the only known ant species to form pulling chains when transporting large prey items, and these chains exhibit a unique and puzzling branched structure (PEETERS & DE GREEF 2015, MIZUNO & al. 2022). However, nothing is known about the individual-level rules underlying the emergence of these structures.

ANDERSON & al. (2002) proposed a classification of self-assemblages based on their overall “complexity”, measured as a combination between the number of functional adaptations that the structure displays and the importance of individual arrangement within the aggregation. That is, simpler structures are the ones where the arrangement of individuals is close to random and that display fewer functional adaptations once formed. In this classification, rafts and swarm clusters are considered simpler than bivouacs and pulling chains. Recent studies have shown, however, that these structures are far from simple, displaying several functional and architectural adaptations that are critical for their functionality (MLOT & al. 2011, FOSTER & al. 2014, PELEG & al. 2018, WAGNER & al. 2021, PETERS & al. 2022, SHISHKOV & al. 2022). Based on the classification proposed by ANDERSON & al. (2002), we suggest *Eciton* army ants’ plugs, bridges, and scaffolds to be simpler aggregations than rafts and swarm clusters. A phylogenetic analysis of the evolution of self-assembly behaviour will provide important results for our understanding of the evolution of these structures.

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