THE ROYAL
SOCIETY

Self-assembly, self-organization and division of labour

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The prospect of generic principles of biological organization being uncovered through the increasingly broad use of the concepts of 'self-assembly' and 'self-organization' in biology will only be fulfilled if students of different levels of biological organization use the same terms with the same meanings. We consider the different ways the terms 'self-assembly' and 'self-organization' have been used, from studies of molecules to studies of animal societies. By linking 'self-assembly' and 'self-organization' with division of labour, we not only put forward a distinction between the underlying concepts but we are also able to relate them to the question: Why has a certain structure been favoured by natural selection? Using the particularly instructive case of social resilience in ant colonies, we demonstrate that the principle of self-organizing self-assembly may apply to higher levels of biological organization than previously considered. We predict that at the level of interactions among organisms within the most advanced animal societies, specialization through learning has a crucial role to play in reassembly processes. This review may also help important commonalities and differences to be recognized between ordering mechanisms up to the social level and those further up the biological hierarchy, at the level of ecological communities.

Keywords: self-assembly; self-organization; division of labour; social resilience; ant, *Leptothorax*

1. INTRODUCTION

Self-assembly and self-organization are concepts that are being used increasingly broadly in biology from studies of molecules to studies of animal societies (see, for example, Fredericks & Hamilton (1997, pp. 565–566) for a discussion of self-assembly in supramolecular structures and Bonabeau *et al.* (1997) for a review of self-organization in animal societies). The use of these concepts holds the prospect of generic principles of organization being uncovered that can further our understanding of the major evolutionary transitions to different levels of biological complexity, e.g. from single cells to societies (Seeley 1989; Maynard Smith & Szathmáry 1997). However, the full value of these potentially unifying concepts is unlikely to be realized if students of different levels of biological organization use the same terms with different meanings.

The aim of this review is to consider the ways the terms 'self-assembly' and 'self-organization' have been used, to propose a distinction between the underlying concepts and to illustrate the importance of this distinction for uncovering generic principles in the way information is transmitted from one level to another in the hierarchy of biological organization with a particularly instructive case: social resilience in ant colonies (Sendova-Franks & Franks 1994).

The definitions we will adopt here are these:

(i) Self-assembly is an assembly process in which only the constituents of the final structure take part (Miller 1976). By 'take part' we mean 'become incorporated' into the final structure. For example, certain forms of self-assembly may only occur in an aqueous medium but the water is not incorporated into the final structure. Therefore, the water does not take part.

(ii) Self-organization (in biology) is a mechanism for building patterns, processes and structures at a higher level through multiple interactions among the components at the lower level, where the components interact through local, often simple, rules that do not explicitly code for the pattern (Camazine & Deneubourg 1994). In certain cases, in self-assembly, there can be an explicit coding of the final pattern in the constituent parts. Such cases would be ones in which self-assembly does not involve self-organization. However, in many cases, in biology, self-assembly, as defined above, will involve self-organization. A major alternative to both self-assembly and self-organization, which provides further clarification, is template-directed assembly because spatial information that explicitly codes for the completed pattern or structure is externally imposed by a template which is not part of the final structure (Miller 1976; figure 1).

Both self-assembly and self-organization refer to processes in which multiple entities become components of a functional whole. These components could take the form either of distinct units, e.g. cells, or of less well-defined constituents, e.g. diffusing substances within a cell. Many biological systems are made up of well-defined units and it is these systems that are our subject here. The

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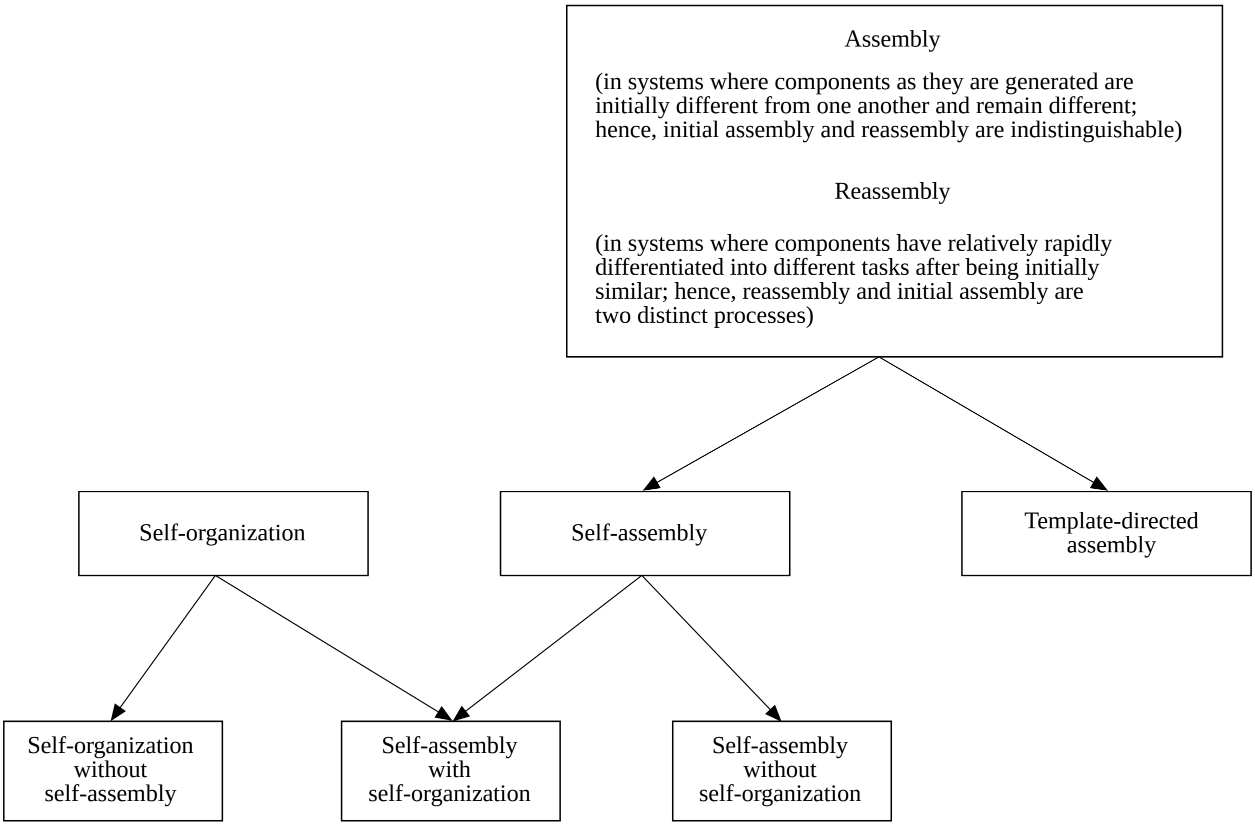

Figure 1. The distinction between self-assembly and self-organization.

components could be either of the same type or of different types. When the components are of, or develop into, different types there is often a division of labour among them that promotes the efficiency of the organization as a whole. For this reason the links between self-assembly and self-organization, and the division of labour will be a major theme in this review.

Division of labour among the members of a production group is an economic principle for increasing the functional efficiency of such a group compared to competitors without a division of labour (Smith 1776). Division of labour is also a fundamental principle of biological organization that has been favoured by natural selection acting on biological systems with multiple components from the subcellular to the supraorganismic level (Maynard Smith & Szathmáry 1997). In biological systems, we suggest the following definition: division of labour occurs when all constituent entities are co-adapted through divergent specialization so that there is a fitness or inclusive fitness gain as a consequence of such specialization. Selection pressures for increased efficiency of such systems have favoured division of labour. Hence, studies of division of labour can be linked to the question: Why has a certain structure been favoured by natural selection? Issues of self-assembly and self-organization are more often associated with the question: How is a certain pattern or structure created? Linking these why and how questions of ultimate and proximate causation—in a sense, combining strategic and tactical issues—shows great promise for a deeper understanding of the evolution of biological forms from cells (Gerhart & Kirschner 1997) to animal societies (Bourke & Franks 1995; Krebs & Davies 1997).

Social resilience is the ability of ant colonies to reassemble after a massive disruption so that workers that had performed different (spatially ordered) tasks re-establish their spatial positions relative to one another and no time and resources are wasted while workers learn new skills (Sendova-Franks & Franks 1994) (see figure 2). There are three ways in which the information for the structure of the workers at the population level can be encoded at the level of the individual worker.

(i) Explicit instructions about where to be in relation to a template, i.e. an additional structure that requires extra encoding (template-directed assembly, figure 1).
(ii) Explicit instructions about which particular individual(s) to interact with (self-assembly without self-organization, figure 1).
(iii) Rules of thumb about how to interact with workers in general (self-assembly with self-organization, figure 1).

We will now introduce the concepts of self-assembly with and without self-organization. One possibility for self-assembly is for each component to carry explicit coding for the type of component with which it should interact. Such coding would be the key to how each component finds its appropriate position in the greater whole. However, in such a scenario, production is potentially wasteful because a single missing component or a single error in the information it carries would render the greater whole dysfunctional. The second possible form of self-assembly involves self-organization. In such cases the components are able to interact potentially with all of the other types of component. We will argue here that this type of self-assembly involving self-organization should, all else being equal, have been favoured by natural selection. This is because such self-assembly through self-organization is effectively simpler, more robust, more secure against failure and is likely to have the capacity for self-repair.

We will now use a highly abstract example to illustrate the differences between (i) self-assembly with explicit coding of the final structure in the components, and (ii) self-assembly through self-organization.

Consider that the complete structure is the series of integers from 1 to 100 arranged from left to right in increasing order. If this was to be achieved by (i) self-assembly with explicit coding, the position of each number would be explicitly coded in its own behaviour. Here the number 50, for example, carries an explicit instruction. The instruction could be one of three types: (a) that it must be positioned to have as its left neighbour 49 and as its right neighbour 51, (b) that it must be immediately on the left of 51, or (c) that it must be immediately on the right of 49. In this example, of self-assembly with explicit coding, if a single (intermediate) integer was missing no single global structure could be produced.

Contrast this with (ii) self-assembly though self-organization. Suppose that there is a self-sorting procedure which results in the integers from 1 to 100 becoming arranged from left to right in increasing order. Here a sorted sequence would result even if many integers were missing because they do not have explicit coding about specific neighbours. In this case of self-assembly through self-organization, each number might simply have the rule to stay where it is when it has a larger number to its right and a smaller number to its left (otherwise it should move, left or right, as appropriate). In this second case, all that matters are the relative values of its neighbours.

These examples are abstract, but they make clear the distinction between the presence or the absence of explicit coding. The former can yield a precise pattern but errors would lead to complete dysfunctionality. The latter yields a generic, more loosely structured, pattern and is likely to be more failure-secure. Recall the example of self-assembly with explicit encoding: the global structure cannot assemble if a single component has a fault in its specific instructions (see (i) above). By contrast, consider the example of self-assembly with self-organization: if one of the components fails, the global structure will have one component out of place, but the remaining components can still assemble into a structure (see (ii) above). Later we will argue that social resilience in ant colonies, for example, is based on self-assembly through self-organization. This argument leads to the prediction that specialization through learning is likely to be of crucial importance in the assembly of organisms into societies.

We will now begin to consider, in depth, how the concepts of 'division of labour', 'self-assembly' and 'self-organization' are related to one another. We shall consider in turn how molecular biologists, developmental biologists and supraorganismic biologists (i.e. those concerned with the most highly integrated animal societies, recognized as superorganisms or supraorganisms; Seeley 1989; Wilson & Sober 1989) have used these terms either in a similar way or in different ways.

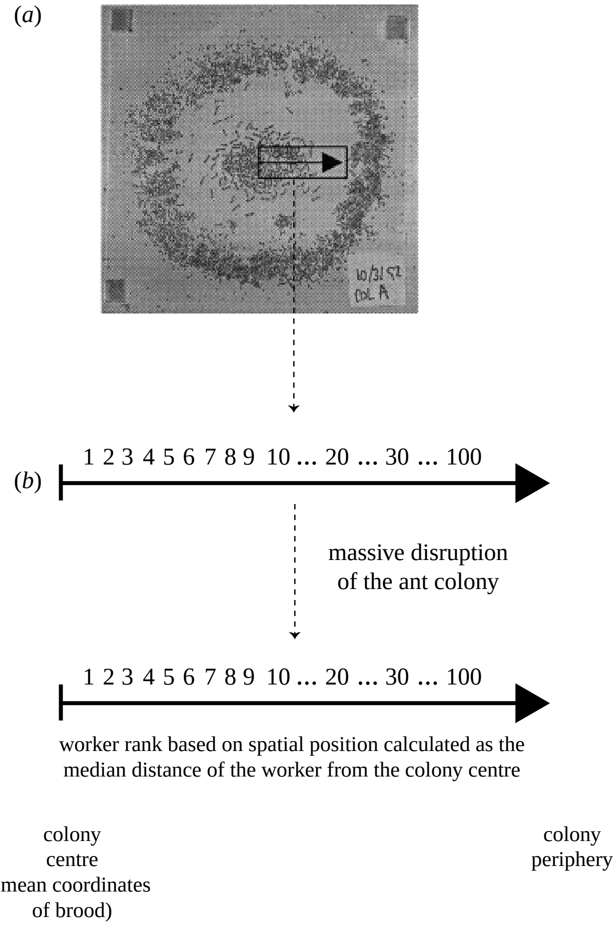

Figure 2. Social resilience in ant colonies. (*a*) A view from above of a *Leptothorax* ant colony nesting between two microscope slides separated by four 1-mm thick corner pieces. The perimeter wall built out of sand granules, the brood pattern and the distribution of the workers have a radial symmetry. Worker spatial position, i.e. spatial fidelity zone, along the radius (from the colony centre to its periphery) is correlated with worker task. (*b*) After massive colony disruption workers re-establish their relative spatial positions and tasks with great fidelity.

2. DIVISION OF LABOUR

We will first consider the division of labour, because this can be related most easily to efficiency and therefore ultimately to selective advantage. The modern usage of the term 'division of labour' comes from the studies of economics in human societies by Adam Smith (1776):

> 'This great increase of the quantity of work which, in consequence of the division of labour, the same number of people are capable of performing, is owing to three different circumstances; first, to the increase of dexterity in every particular workman; secondly, to the saving of the time which is commonly lost in passing from one species of work to another; and lastly, to the invention of a great number of machines which facilitate and abridge labour, and enable one man to do the work of many.'

(Adam Smith (1776) in Bourke & Franks (1995, p. 401))

In biological systems, division of labour occurs when all constituent entities are co-adapted through (enhanced mutually beneficial) divergent specialization so that there is a fitness or inclusive fitness gain as a consequence of such specialization. The steps (either in evolutionary time or through learning) to such a division of labour could be as follows.

(i) There is an immediate and purely fortuitous advantage to one party, A from associating with another party, B.
(ii) The other party, B, changes to take advantage of the presence of A.
(iii) Party A changes too because some of its traits are now redundant and hence it can re-allocate resources and specialize further. These changes, both to A and B, could occur over evolutionary time or during the lifetime of the individuals involved, i.e. behaviourally through learning.

Here we will consider division of labour that has taken place over evolutionary time. In some cases such division of labour occurs among entities which are initially different from one another. For example, consider mitochondria and ribosomes. They are both organelles that contribute in different ways to the collective functioning of a cell. They are also entities that, as they were generated, were initially different from one another and remain different from one another (Luck 1965, mitochondrial biogenesis; Darnell *et al.* 1990, pp. 273–274, ribosome assembly). In other, arguably more interesting cases, however, the division of labour occurs among entities that are initially similar but relatively rapidly differentiate into different roles or tasks. Consider, for example, the early stages in the development of a metazoan embryo. During these early stages a process of regional specification leads to the differentiation of initially similar and totipotent cells into regions of different cell types (Slack 1991).

When division of labour occurs among entities that are initially different from one another there are no obvious merits in recognizing the process of reassembly as distinct from the process of initial assembly. To clarify this, first consider a case without a division of labour. When a polypeptide, for example, assembles initially or reassembles after denaturation the two processes are exactly the same because the subunits are initially different and remain different. In this case, both initial assembly and reassembly are based on such differences. This can also be true for supramacromolecular structures and cell organelles (Miller 1976), and higher levels of organization in which there is a division of labour.

When division of labour occurs among entities that are initially similar but later differentiate into different roles or tasks, although both initial assembly and reassembly still lead to the same final structure, there is a good reason to distinguish between the two processes because different mechanisms are involved. Consider, for example, the classic experiments on the reconstruction of 'primitive sponges'. In 1907, Wilson discovered that when a *Microciona* sponge is squeezed through a fine silk mesh so that its cells are dissociated, the cells can re-aggregate back into a functional sponge. He was convinced that such reconstruction was accompanied by processes of dedifferentiation and redifferentiation of the reaggregated cells (Wilson 1907). Repeating this experiment on *Sycon*, Huxley was the first to recognize that, since isolated cells of only one type could not reconstruct a functional sponge, there was no redifferentiation but instead the existing cell types reorganized themselves by returning to the same positions relative to one another (Huxley 1911, 1912, pp. 96–97; see also Curtis *et al.* 1982).

This example is an excellent illustration of the difference between the two types of assembly process associated with the division of labour among entities that are initially similar. The first issue concerns the proximate mechanisms whereby initially similar entities differentiate into different roles or tasks. This is the process of initial assembly. (For example, this would be the initial differentiation of the cells in a sponge.) Second, there is the issue of the proximate mechanisms whereby, as a consequence of their differentiated forms, different types of entities can re-establish their positions relative to one another. This is the process of reassembly. Indeed, Wilson's (1907) explanation of the reconstruction of the *Microciona* sponge was dismissive of any process other than one identical to the process of initial assembly. It was Huxley's (1911) experiments that demonstrated, for the first time, the existence of the distinctly new process of sponge reassembly. In developmental biology this distinction has been expressed by Driesch's (1907) dictum for the developing embryo: that the fate of a cell is a function of its position. By contrast, Huxley pointed out that the results from his reassembly experiments on *Sycon* were an instance where the position of a cell was a function of its fate, i.e. its differentiated state (Bonner 1974, p. 186).

So far we have recognized the existence of two types of division of labour: (i) among entities that are initially different, and (ii) among entities that are initially similar but later differentiate into different tasks. Furthermore, we have argued that a distinction between the processes of initial assembly and reassembly is instructive only when the entities are initially similar and differentiate later. Now we shall consider in turn how this applies to interactions among entities at different levels of biological organization.

At the level of molecular and subcellular interactions, division of labour is of the first type, that is, among entities that are initially different.

At the level of cellular interactions, division of labour in the early stages of development is of the second type, that is, among entities that are initially similar but later differentiate into different tasks. The fundamental issue of such initial assembly is best summarized by Wolpert's classic French flag problem (Wolpert 1969). It poses the question: What mechanism would ensure that a line of totipotent cells would always have a French flag pattern—a third blue, a third white and a third red? (Wolpert 1996) A possible answer lies in the idea that each cell acquires a positional value (positional information) related to its place in the developing system, which it then interprets to generate a particular differentiated state.

At the level of interactions among organisms in a colony of eusocial insects, for example, division of labour is of both types. In evolutionary terms, division of labour, in such cases, occurred first and foremost over reproduction. The next stage in the evolution of division of labour is division of labour over non-reproductive tasks. Such a division of labour over 'quotidian' tasks occurs in almost all advanced eusocial insect societies. It is useful to distinguish two forms of differentiation among workers. The first occurs when there are physical morphs and hence there is physical polyethism. Here there is a division of labour among entities that are initially different and this occurs in termites and in only 20% of ant species (Bourke & Franks 1995, p. 417). By contrast, a much more common division of labour is among individuals of the same physical morph. Here the division of labour is among entities that are initially similar and later differentiate into different tasks.

Certain authors have argued that in insect societies with a single physical morph of worker, division of labour is based on a causal relationship between age and task and hence in such societies there is age polyethism (for a review, see Hölldobler & Wilson 1990, p. 307). This implies that the age distribution of workers determines the division of labour. There is, however, overwhelming evidence for flexibility in the division of labour which is hard to reconcile with such 'hard-wired' age polyethism (Franks 1994). Perhaps one of the most striking examples of this comes from swarming in honeybees. Swarming is an essential stage in the life cycle of a honeybee colony. During swarming the parent colony does not split equally either in terms of the total number of workers or in terms of the ratio of different age groups. Thus, the swarm that leaves the hive contains approximately 70% of the original adult worker population while the daughter colony that remains in the hive contains the very young and the very old workers (Seeley 1985, p. 60). Nevertheless, all such remaining workers have to perform the full range of quotidian tasks in the colony. For further review of flexibility in the division of labour in social insect colonies see Robinson (1992), Bourke & Franks (1995) and Gordon (1996).

Therefore, given the propensity of individuals to perform different tasks flexibly during different parts of their lives (temporal polyethism), the key issue in the initial assembly of social insect colonies is how populations of workers are matched to populations of tasks. This can be summarized through the approach taken by the foraging-for-work model for task allocation (Tofts & Franks 1992). It poses the question: What is the simplest algorithm that would distribute the appropriate number of workers to the available tasks? (Tofts & Franks 1992; Tofts 1993) The foraging-for-work algorithm envisages a linear production line along which individual workers first find their positions according to supply and demand and only then differentiate into performing the appropriate tasks. This can be seen as an example in which the components (the workers) are initially similar and initial assembly occurs through self-organization in which workers become differentiated into the different tasks associated with their spatial positions.

3. SELF-ASSEMBLY

The concept of self-assembly originated in the search for principles of biological organization that began at the level of molecular interactions (Caspar 1966) inspired by the structure and function of DNA (Watson & Crick 1953*a*,*b*) and the quantum physicist's insight that life has the propensity to produce order from order (Schrödinger 1944, pp. 68, 80). At present, there is a well-established distinction (Wood *et al.* 1981, pp. 79–80) between self-assembly (as in ribosomes and certain viruses) and template-directed assembly (as in cell walls, membranes and chromosomes). The value of the distinction between self-assembly (in which only the constituents of the final structure take part) and template-directed assembly (in which spatial information is imposed externally by a template which is not itself part of the final structure, Miller (1976)) follows. Where self-assembly operates, a direct sequence of causal steps could, at least in principle, be traced from the gene to the form of the molecular aggregate (Miller 1976). Furthermore, self-assembly might be economical in terms of its genetic encoding (since it does not require extra coding for a template) and robust against genetic errors as suggested for small viruses (Crick & Watson 1956).

The question remains how biological order is maintained further up the hierarchy of biological organization, at the level of cellular interactions. As Huxley pointed out, while pondering the fascinating ability of *Sycon* sponges to reassemble after cell dissociation (Huxley 1912, p. 93), the answer to this fundamental question is in the mechanisms that organize minor biological entities (cells) into a major functional whole (an organism). Thus, an important experimental approach to the study of such mechanisms, in terms of proximate causation, is to investigate whether and how dissociated component entities can reassemble back into a functional biological whole.

In § 2 we highlighted the distinction that exists between the processes of initial assembly and reassembly when division of labour occurs among entities that are initially similar, as at the level of cellular interactions and at the level of interactions among organisms. At these two levels, the process of reassembly involves already differentiated entities and hence has similarities to the process of assembly at the molecular and subcellular level (figure 1).

Since Wilson's (1907) and Huxley's (1911, 1912) experiments on sponges, it has been established that hydra and the early sea-urchin embryo can also reassemble, but the higher animals do not have this capability (Wolpert 1993, p. 25). Dissociated cells from the embryonic organs of vertebrates, however, can sort themselves into their original tissue organization (Townes & Holtfreter 1955; Medoff & Gross 1971). It is widely accepted that a process similar to self-assembly, could be responsible for the sorting of cells of different types in culture and could play an important role in cell re-arrangements during morphogenesis (Bard 1992, pp. 184, 254–256) as in, for example, the morphogenesis of the neural tube in teleost fish (Cooper *et al.* 1996). Indeed, in Waddington's (1962, p. 88) classification, self-assembly comprised one of the four groups of processes responsible for the generation of biological form. These are: by units (self-assembly), by instruction, by template and by condition. The underlying mechanisms in cell sorting have been identified as cell motility and differential cell adhesion. There are qualitatively different cell adhesion molecules (CAMs; Edelman & Gallin 1987) but a quantitative difference in cell adhesion is sufficient to drive cell sorting (Steinberg 1963). At present cell sorting is considered to be one of the clearest examples of the principle of self-organization in morphogenesis and a number of models have been developed, the most recent of which considers explicitly the movement of cells as a stochastic process (Mochizuki *et al*. 1996).

One of the few known clear examples of reassembly of a supraorganism is social resilience in ant colonies (Sendova-Franks & Franks 1994). There is growing evidence to suggest that the mechanisms underlying social resilience also constitute a self-assembly process. Indeed, parallels between a metazoan organism and a social insect colony were first drawn in modern times by Wheeler (1911). Furthermore, Wilson (1985) coined the term 'sociogenesis' for social insects by analogy to morphogenesis in metazoans. He envisaged that the meshing of comparable information from developmental biology and sociobiology would reveal general and exact principles of biological organization. Wilson (1985) defined sociogenesis as the process by which colony members undergo changes in caste, behaviour and physical location associated with colonial development.

Colonies of the ant genus *Leptothorax*, in which social resilience was first demonstrated, have proved an ideal experimental subject for studies of sociogenesis (Franks *et al*. 1992; Franks & Sendova-Franks 1992; Sendova-Franks & Franks 1993). They live in comparatively small societies (the number of workers being of the order of hundreds rather than thousands or millions), build relatively simple nests and hence entire colonies can be easily collected. Best of all, they nest in approximately flat crevices in rocks and can be cultured in extremely thin glass nests. Thus, in the laboratory, *Leptothorax* colonies can be housed under conditions that both closely resemble their natural nest geometry and allow all individuals to be observed simultaneously for months and even years. This provides an opportunity to investigate experimentally not only the social profile but also the physical position of individually recognizable workers (Sendova-Franks & Franks 1995*a*). Therefore, the study of positional effects in sociogenesis (Wilson 1985) analogous to that of positional information in the development of form in metazoans (Wolpert 1969, 1996) can be comparatively easy and rigorous.

When we performed dissociation experiments on *Leptothorax* colonies analogous to Huxley's on *Sycon*, by using uniquely marked individuals, we found that workers re-established, with great fidelity, their positions relative to one another (along the radius from the colony centre to its periphery). That is, we found that ant workers could also reorganize themselves back into a functional colony without dedifferentiation and redifferentiation. We termed this phenomenon social resilience (Sendova-Franks & Franks 1994).

The analogy between the reconstruction of sponges and social resilience in ant colonies is not totally surprising. In a general sense it was predicted by Allee *et al*. (1949, p. 427) who stated that 'the social insect colony has a pattern [of functions and integration] significantly similar to that of a lowly multicellular organism such as a sponge'.

An important distinction for understanding the proximate mechanisms underlying social resilience, as at the other levels of biological organization, is between mechanisms in which only the constituents of the final structure take part in the assembly process and those in which spatial information is imposed externally by a template which is not itself part of the final structure. The final structure of interest here is the configuration of the worker population without the queen or the brood. Considering the worker population as a structure in its own right facilitates analysis of social organization and is justified both in terms of proximate and ultimate mechanisms. For example, the queen, who is both morphologically and physiologically different from the workers, resides in the colony centre and often has different reproductive interests to the workers in terms of sex ratio, constitutes a potential source of a pheromone gradient and hence could provide a template for colony reassembly. With such a template, workers would be able to return to their places relative to one another by initially learning and then re-establishing their own positions along an olfactory gradient. The brood, which is organized in concentric circles with the smallest items in the centre and the largest on the periphery (Franks & Sendova-Franks 1992) also constitutes a potential template for colony reassembly. The brood pattern is reconstructed after colony emigration in a process that probably involves self-organization (Franks & Sendova-Franks 1992). It is possible that after, brood sorting workers could return to their relative positions by using the brood pattern as a template, e.g. by having learnt the particular odours of the different brood types. Different types of brood also represent different tasks and sorting according to brood would put workers back into locations and/or task zones in which they had already developed specialized skills.

There are two main functional reasons why it is important to make a distinction between such potential templates and the possibility that workers could re-establish their spatial positions relative to one another without any information from the environment.

(i) Template-directed assembly would imply that workers require outside information in order to resume their relative spatial positions and task specializations in the day-to-day work of the colony.
(ii) Self-assembly would point to the possibility that such day-to-day differentiation of workers has been internalized.

If such internalized differentiation is a quantitative variable such as, for example, the mobility level of the workers, self-assembly would indicate a higher level of colony flexibility combined with a maximum conservation of social relationships among workers. Indeed, if social resilience is based on quantitative worker variables, this would provide not only a very simple mechanism but also one that is robust, failure-secure and self-repairing. For example, quantitative variables that allow workers to rank themselves would still operate when a substantial proportion of brood, workers or indeed the queen have been lost during the emigration. Furthermore, with regard to life-history strategies, the ability to conserve worker social relationships may be essential for efficiency to be maintained in the face of reproductive conflict during the three years of colony life after the queen dies (Franks *et al*. 1990).

If social resilience constitutes a self-assembly process, it might be the case that when the ants emigrate to a new nest they sort themselves along a radius from the centre of the colony to its periphery depending on their relative mobility. Following encounters, neighbouring ants may exchange positions so that less mobile ones move towards the centre and more mobile ones move towards the periphery. In this way, relatively mobile ants may 'diffuse' outwards and relatively immobile ants may 'diffuse' inwards until each is sandwiched between a more mobile and a less mobile neighbour. (This is reminiscent of cell sorting; Steinberg 1963.) Note that in this hypothesis the colony centre is not provided extrinsically but intrinsically, by the propensity of ants from the same colony to aggregate.

4. SELF-ORGANIZATION

The theory of self-organization, originally developed in the context of physics and chemistry, is now widely applied in studies of the proximate mechanisms of social life in animals and social insects in particular (Bonabeau *et al.* 1997).

A comparison of the definitions of self-organization and self-assembly (see §1) shows that they are two different processes. In many cases, however, both may operate together. Recognizing both of these points should help to avoid some of the confusion between the concepts of self-assembly and self-organization in the literature. For example, in supramolecular chemistry the two concepts are generally used completely interchangeably, the emphasis being on the non-covalent interactions between molecules and the spontaneity of the assembly process (Fredericks & Hamilton 1997, pp. 565–566).

In their recent book on developmental biology, however, Gerhart & Kirschner (1997, pp. 146, 151) make a distinction between the two concepts in the light of their review of the exploratory behaviour of certain biological systems, such as ant foraging, microtubule assembly, the generation of specificity in the immune system, development of the nervous system, the generation of new blood vessels in vertebrates and the generation of the tracheal system in insects. They view self-assembly as a process that tends to generate a single well-defined structure uniquely determined by the number and size of the components, and by the geometry and strength of interactions. By contrast, Gerhart & Kirschner (1997, p. 151) view self-organization as a process that will generate structures under a wider set of conditions where the rules tend to be more general and the structures more variable. They also suggest that there is an aspect of self-assembly that implies an energy minimization, whereas a stable structure in a self-organizing process is often accompanied by energy dissipation and gain and loss of material. Accordingly, they consider the above examples of the generation of exploratory structures as examples of self-organization but not of self-assembly.

A crucial distinction between self-assembly and self-organization is implicit in Gerhart & Kirschner's (1997, pp. 146, 151) viewpoint but needs to be spelt out as we did earlier (figure 1, see §1). Namely, that in self-assembly it is the initial differences and/or relationships among the components that encode the global structure of the assembled whole, while in self-organization such initial encoding is not a necessary condition.

A key feature of certain self-organization studies is that they show how structures could be generated from interactions among identical components (which may later differentiate during or after the global pattern has been produced). The philosophy of self-organization theory (in common with almost all theory) is that it tries to explain as much as possible with as little as possible. Hence, unless it is obvious that different component types are required for a self-organizing process to occur as in the Belousov–Zhabotinskii reaction (Murray 1989, p. 179), for example, then it typically poses the question: What can be achieved by identical components? Thus typically in such models of self-organization the interacting entities are (initially) designated as being identical to one another (e.g. Theraulaz *et al.* 1998).Of course, these models do not imply that in nature all the individuals are identical, rather they imply that the differences among them may not be important for the generation of a particular structure or pattern. For example, in army ant foraging raids there is a tremendous polymorphism among the foraging population (Franks 1985) but crucially such polymorphism is not necessary for the formation of the foraging raids, as revealed by modelling which shows that identical entities can produce the foraging pattern (Deneubourg *et al.* 1989; Franks *et al.* 1991).

By contrast, as we have shown in §3, differences among the components can be a necessary condition for the formation of the global structure because its form is encoded by these differences. Our claim here is that where these differences are quantitative, the process may still involve self-organization because the global pattern is not explicitly encoded in the interactions among its components. Thus, self-assembly that is based on non-explicit (non-specific), quantitative interactions is self-organizing (consider the earlier example of the self-sorting integers from 1 to 100). For example, given this distinction, cell sorting is a form of self-organizing self-assembly precisely because the underlying mechanisms are a combination of cell motility and differential cell adhesion provided by cell-adhesion molecules where quantitative differences alone are sufficient (Steinberg 1963). Our hypothesis, based on the working assumption that differential worker mobility in combination with the propensity of ants from the same colony to aggregate is the underlying mechanism for social resilience in ant colonies, implies that social resilience is also a self-organizing self-assembly process. Another point that needs to be recognized is that at higher levels of biological organization self-assembly is even less deterministic than at the molecular level and indeed different numbers and types of components can be involved, although, crucially, it is still the differences among the components that encode the pattern.

Thus, we would suggest that the examples of the generation of ant foraging trails or of specificity in the immune system, etc., that Gerhart & Kirschner (1997, pp. 146–198) discuss are examples in which entities that are initially similar differentiate into different tasks through self-organization. If the same structures were to reassemble so that entities of different types could re-establish their positions relative to one another, the underlying processes would be the same in principle as initial assembly at the level of molecular interactions.

Such reassembly would be a self-organizing self-assembly only if the already differentiated constituents of the final structure were able to find their relative positions back into a functional whole through multiple interactions that do not explicitly code for the global pattern. For example, it is, at least in theory, possible that social resilience is based on a mechanism whereby workers are able to learn the identity of their neighbours. According to the definitions above, a mechanism of this kind would comprise self-assembly but not self-organization, because the global pattern would be explicitly encoded in the unique interactions of unique neighbours.

A major alternative to self-assembly and self-organization is template-directed assembly. Note, however, that template-directed assembly could be employed in a subsequent self-organizing process and vice versa, a self-organized pattern could later be used for template-directed assembly. For example, nest building in termites and ants involves a sequence of steps consisting of template-directed assembly followed by self-organization (Franks & Deneubourg 1997; Bonabeau *et al*. 1998). Thus, certain termite queens produce a pheromone that determines where the wall of the royal chamber, in which the queen will become encased, will be built.

The queen's building pheromone probably designates the zone, neither too close nor too far from her own body, within which the wall should be formed. However, building within such a zone can be purely self-organizing. In this way, the termites could use a template coupled to later self-organization (Bonabeau *et al*. 1998). Alternatively, a pattern or structure that was based on self-organization could later be used as a template. For example, the pattern generated by the self-organized process of brood sorting following emigration in *Leptothorax* ant colonies (Franks & Sendova-Franks 1992) could, in principle, subsequently be employed as a template in the reassembly of the workers themselves.

5. IMPLICATIONS AND CONCLUSIONS

Our aim in this review has been to consider the ways in which the terms 'self-assembly' and 'self-organization' have been used in biology, to propose a distinction between the underlying concepts and in view of this distinction to illustrate their generic applicability to different levels of biological organization with the case of social resilience in ant colonies. We approached these two concepts in the context of division of labour, because this can be related most easily to efficiency and therefore to selective advantage of entities with differentiated components over entities with undifferentiated components. Here we will summarize the new generic insights that result from these considerations.

There is a distinction to be made between division of labour among units that are initially different and division of labour among units that are initially similar and differentiate later. This distinction is important for recognizing that the principle of reassembly of already differentiated units back into a functional whole is valid at all levels of biological organization with all its inherent economy of information, fault-tolerance and robustness.

The distinction between self-assembly and template-directed assembly originating in molecular biology has already been adopted in developmental biology and as this paper demonstrates will also be instructive in the understanding of the mechanisms underlying reassembly at the supraorganismic level.

Self-assembly and self-organization are two distinct processes (figure 1). However, at all levels of biological organization many (perhaps, the majority) of self-assembly processes are also self-organizing. There are two requirements that appear fundamental to a self-organizing self-assembly: mobility of the smaller entities and a sorting procedure based on differential values of a quantitative variable. (In addition, as Gerhart & Kirschner (1997, p. 151), point out, the mechanisms that eventually keep components in their 'appropriate' positions may well involve energy minimization, see also Maynard Smith & Száthmary (1997, p. 206).) Thus, at the level of interactions among molecules, a biological macromolecule moves from one place to another through diffusion until it collides with another macromolecule and establishes a 'weak' bond through non-specific non-covalent interactions between chemical groups (Bonner 1974, pp. 174–175).

At the level of cellular interactions, movement is also considered to be a stochastic process in which cells arrive in a particular position through differential adhesion to other cell types (Bard 1992, p. 265). Morphogenetic strategies appear to have evolved towards the use of stochastic processes for the generation of form. Thus, many 'evolutionarily older' organisms (with the exception it seems of simple sponges), such as the nematode *Caenorhabditis elegans*, seem to develop in a precisely defined way, although recent research reveals more flexibility than previously thought (Gerhart & Kirschner 1997, pp. 260–268, 343–344). Cell movement and hence self-assembly during morphogenesis tend to be associated with 'evolutionarily younger' organisms and may represent a developmental process that has only relatively recently been capitalized on by evolution (Bard 1992, p. 265).

At the level of interactions among organisms, the individuals are relatively complex and autonomous. They are usually also highly mobile. The trajectories of individual animals can be influenced by both interactions with objects in their surroundings and interactions with other individuals. In the case of self-assembly in ant colonies that we have examined here, workers might hypothetically reconstitute their relative positions and be kept in place through a sorting mechanism based on their relative mobility and their propensity to aggregate. There are two key issues. First, how a worker's relative mobility is influenced by her task and position in the original nest. In this regard, it may be instructive to proceed on the assumption that movement is stochastic and then to explore how much of the observed mobility levels could be explained only in terms of interactions between workers and tasks. It is highly likely that in addition to the interactions visible to us there are also those that we are unable to observe directly (Sendova-Franks & Franks 1995*b*). The second issue is how a worker's particular level of mobility from the old nest is internalized (encoded in the individual) so that it can be re-established in the new nest? As far as this issue is concerned, a positive feedback mechanism such as, for example, the ability of individuals to learn (Deneubourg *et al*. 1987; Theraulaz *et al*. 1998), which is common at this level, could play a crucial role in the mechanism by which individuals retain their relative mobility level.

It is indeed possible that worker differentiation is internalized, in which case workers would be able to restore their relative positions without reference to the environment. This raises the question: What is the functional significance of this phenomenon? By analogy to morphogenesis the prediction can be made that in ant colonies with higher numbers of workers and perhaps a higher level of differentiation and integration, the process of self-assembly is used in movements of groups of workers with similar mobility levels during sociogenesis. Emigrations from an old to a new nest site in colonies of all sizes could be considered as an extreme example of such sociogenetic movements where the re-establishment of the relative spatial positions of workers with different tasks saves time and resources from being wasted by workers learning new skills (Sendova-Franks & Franks 1994).

Our arguments about the role of reassembly processes at the level of interactions among organisms have been illustrated with social resilience in ant colonies, but they may be more generic. There has been a recent call, for example, to consider all animals as arranged along a sociality continuum (Sherman *et al.* 1995), of which social insects can be regarded as certain, albeit often extreme, examples. Both recent theoretical work and empirical studies have focused on the importance of spatial structure in the evolution and maintenance of social behaviour. For example, on the one hand, Nowak *et al.* (1994, 1995) have shown, through theoretical studies, the importance of spatial structure on the players in a prisoner's dilemma so that different behavioural strategies are maintained without the requirement of complex behaviour on the part of individuals. On the other hand, Palomares & Delibes (1993) and Schwede *et al.* (1993), for example, have demonstrated empirically the spatial structure of animal societies. Data also exist on reassembly processes on, among others, migratory seabirds. In Cullen's (1957) classical work on colonies of kittiwakes, for example, there is evidence of fidelity of breeding pairs to particular cliff ledges, while individuals in returning flocks of barnacle geese display site fidelity (Black *et al.* 1991; Black & Prop 1996).

Caution at the above-organismic level should be taken, however, to recognize the distinction among the three steps to division of labour we pointed out earlier. To illustrate this distinction we will use as an example observations made in North America of badgers and coyotes forming hunting pairs (Kiliaan *et al.* 1991). Badgers are better at digging out small mammals, and coyotes are better at long distance detection (vigilance) of large predators that could kill them (or a badger). The coyote can catch excavated prey that can outrun a badger. Consider a lone badger; suppose that it spends 50% of its foraging time excavating (ground squirrels) and 50% being vigilant. Consider a lone coyote; suppose that it spends 50% of its foraging time chasing prey, 30% digging for prey and 20% being vigilant. When the badger and the coyote are together the following associations could exist.

(i) Spatial association. This may lead to one or each partner gaining in fitness, for example, through a reduction in the proportion of time each spends being vigilant. There is, however, no co-adapted specialization here and hence no division of labour. Similar examples are: a mixed-species shoal of fishes where fishes are size-assorted, thus possibly minimizing predation risk and maximizing foraging efficiency (Krause *et al.* 1996), but with no evidence for specialization; and a group of birds or mammals where there is a negative correlation between group size and antipredator vigilance behaviour, irrespective of whether this correlation can or cannot (Elgar 1989) be attributed to individuals directly changing their behaviour as a function of group size, since there does not appear to be any specialization in vigilance.

(ii) One partner changes its behaviour. For example, consider that the badger now spends 80% of its time digging and 20% being vigilant, while the coyote's behaviour remains the same. In this case both partners gain in fitness because the badger digs up many more prey, some of which it eats and some of which escape and are eaten by the coyote, but there is no mutual division of labour. A similar example is a mixed-species flock of birds where individuals of one species, in addition to associating as close neighbours with individuals of another species, may modify their foraging behaviour on joining the flock. This may lead to both species gaining even greater feeding benefits from flocking than the benefits accrued solely from spatial association (Latta & Wunderle 1996).

(iii) Both (all) partners change behaviour through mutual specialization. For example, the badger now spends 80% of its time digging and 20% being vigilant, while the coyote now spends 70% of its time chasing prey and 30% being vigilant. Thus, the badger gains better warning from impending danger from the coyote, while the coyote benefits from obtaining ground squirrels escaping the digging badger. There is a fitness gain for both partners, as in (ii), but here, additionally, there is a co-adapted specialization by both partners. Therefore, there is also a division of labour.

Discriminating among these possibilities is important because there is similarity in proximate mechanisms but dissimilarity in ultimate mechanisms between, for example, our hypothesis of differential worker mobility and a differential mobility in a mixed-species shoal of fishes where the fishes are of different sizes and swim with different speeds (Krause *et al.* 1996). In the former, there is a division of labour among entities (workers) that are initially similar but later differentiate in the context of a group (colony) function. In the latter, the fishes are initially different and there does not appear to be any division of labour.

Finally, reassembly processes of, what are effectively, populations of organisms could be helpful in understanding ordering mechanisms even further up the biological hierarchy, at the level of ecological communities. Indeed, the term 'assembly rule' has been widely used to describe the process by which populations in a community fit together (Drake 1990).

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