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**Architecture, Space and Information in Constructions Built  
by Humans and Social Insects: a Conceptual Review**

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# Architecture, Space and Information in Constructions Built by Humans and Social Insects: a Conceptual Review

## Keywords

Space, Information, Architecture, Perception, Social Systems.

## Abstract

The similarities between the structures built by social insects and by humans have led to a convergence of interests between biologists and architects. This new, de facto interdisciplinary community of scholars needs a common terminology and theoretical framework in which to ground its work. In this conceptually oriented review paper, we review the terms “information”, “space” and “architecture” to provide definitions that span biology and architecture. A framework is proposed on which interdisciplinary exchange may be better served, with the view that this will aid better cross fertilisation between disciplines, working in the areas of collective behaviour and analysis of the structures and edifices constructed by non-humans; and to facilitate how this area of study may better contribute to the field of architecture. We then use these definitions to discuss the informational content of constructions built by organisms and the influence these have on behaviour, and vice versa. We review how spatial constraints inform and influence interaction between an organism and its environment, and examine the reciprocity of space and information on construction and the behaviour of humans and social insects.

## 1. Introduction

Living systems are both constructions and constructors [1,2]. At the fundamental level, organic molecules self-assemble into organic compounds (e.g. proteins, DNA) that build organelles and cells [1]. Cells in turn can assemble themselves into tissues, organs, and ultimately fully functional organisms [3–8]. Organisms modify their environment to build functional structures that will protect them (e.g. bird nests) and help them acquire the resources that they need for their development, survival and reproduction (e.g. spider web) [9–11]. Finally, organisms in societies can combine their building efforts to achieve constructions that no single individual could produce on its own, as is exemplified by termite mounds and human skyscrapers, which can be several hundreds - or even thousands - times larger than the individuals that build them [11,12].

Social insects in particular have long fascinated biologists by their ability to mold their environment to their needs [13–16]. Some species of ants are known to clear debris and vegetation to form large trail networks the size of a football field, connecting their multiple nests to various resources [17–19]. Others have mastered the art of tunneling to build underground networks of galleries connecting chambers housing their workforce, brood, food stockpiles, and even subterranean fungus garden [20–25]. Many species of ants, termites, bees and wasps build structures by

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3 accumulating material (e.g. wax, saliva-imbibed soil or vegetable fibers) that will form walls, pillars,  
4 floors and ceilings [14,26–35]. Finally, some ants and bees use their own bodies as construction  
5 material, attaching to each other and creating dynamical structures such as bridges, ladders, holds  
6 and temporary nests [12,36–49].  
7

8 The complexity and diversity of structures built by social insects is reminiscent of that of human  
9 beings [50]. Their construction rules are however radically different. Unlike human-made  
10 constructions that are most often composed of inert and standardized units assembled in a precise  
11 order, social insect constructions are built from more plastic and irregular components, and their  
12 assemblage results from distributed processes of self-organization with little to no supervision  
13 [13,51,52]. As a result, their structures are less standardized, but more capable of adjusting their  
14 conformation in response to changes in the conditions in which they are placed [12,37,38,53,54].  
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16 The parallels and divergences between the structures built by social insects and by humans have  
17 sparked a lot of interest in the architectural community [55–60]. The natural world has been an  
18 inspiration for architects since antiquity, with biology becoming a key influence on design thinking at  
19 the turn of the C19th; when the analogical influence turned to interest in how biological systems  
20 develop and evolve (see Mertins, 2007; Steadman, 1983) [61,62]. Coupled with the computational  
21 capacity to simulate natural systems architects are today exploring the self-organising and emergent  
22 morphologies of biological phenomena to rethink how buildings and cities are designed [63–71]. The  
23 emergent, adaptable and situated structures built by social insects offer intriguing insights in  
24 particular for architects to re-evaluate not only the sustainable aspects of the human built  
25 environment but to question the distinction between cognitive phases of human architecture (i.e.,  
26 between design, construction, and occupancy stages) and to think about these as continuous. (see  
27 Soar, 2016) [72].  
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31 Recently, biologists and architects have starting coming together to form a new community,  
32 interested in understanding the construction mechanisms used by social insects and their potential  
33 applications in human-made structures [55,73]. As is to be expected between two disciplines that  
34 have existed in parallel with little interaction, terminology has quickly become the first obstacle to  
35 creating a theoretical framework in which to ground the emerging field. During discussions  
36 preceding the writing of this manuscript, the authors have identified three concepts in particular  
37 that rendered their mutual understanding difficult: architecture, space, and information. In what  
38 follows, we will first try to reconcile the somewhat liberal use by biologists of the concept of  
39 architecture with the more institutional definition that architects have of it. We will then discuss the  
40 concept of space in architecture and biology, and how social systems use space both as a source of  
41 information and a mean to encode social information. Finally, we will discuss the idea of information  
42 itself and the effects of architecture on information flow and processing in social systems.  
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## 46 **2. Scope of the review**

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48 One of the problems with interdisciplinary work is language, and is what may be termed the baggage  
49 individual disciplines bring to the table. Essentially, terminology can be a barrier for interdisciplinary  
50 exchange. Key terms, such as architecture, space and information have long conceptual histories,  
51 such that even their everyday use is awkward. Closer inspection only muddies the water further  
52 because of the way different disciplines claim the high ground with regards their specific outlook.  
53 “Space” for example is from one side an enclosure (i.e. it has boundaries) and the other the void (i.e.  
54 the volume contained within these boundaries). Our capacity to mathematically articulate spatial  
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scenarios gives the impression “space” is something we have generally mastered conceptually, but the fact that a concise definition evades us implies otherwise.

Another case in point is the title of this paper, which is loaded with conceptual connotations. “Architecture”, for example, is principally concerned with the human built environment. It is the practice of designing buildings and articulating how to build the design; not forgetting how to explain the rationale behind the design to demonstrate why that design should be built. Professional architectural societies, such as the Royal Institute of British Architects (founded to facilitate and promote the advancement of architecture) guard the term specifically as referring to buildings designed by architects, and the Architects Registration Board (ARB), the statutory body for the registration of architects in the United Kingdom, protect the term in law. Yet these terms (architecture; architect) are often borrowed to refer to complicated structures and artefacts, such as software applications and circuit boards, recognised as products of intentional design. This trend is particularly apparent within the frame of this special issue, which is concerned with constructions built, particularly, by social insects and comparisons that may be drawn between such structures and the human built environment.

The authors, a biologist and an architect, brought together through their interest in the natural world and specifically the structures creatures (other than humans) construct, have sought to establish a ground on which interdisciplinary exchange may be better served by discussing definitions of fundamental terms that span biology and architecture. Our primary goal is to aid better cross fertilisation between disciplines, working in the areas of collective behaviour and analysis of the structures and edifices constructed by non-humans; and to facilitate how this area of study may better contribute to the field of architecture.

### **3. Toward an interdisciplinary framework**

#### **3.1. Are social insects architects?**

Architecture has many meanings. For instance Steven Holl said, during his acceptance speech for the 2012 American Institute of Architects Gold Medal, that “architecture is an art bridging the humanities and sciences” [74]. Thomas Mayne, at his Pritzker Prize acceptance speech, said that “architecture is a way of seeing, thinking and questioning our world and our place it” [75]. Claiming social responsibility as its most definitive attribute Samuel Mockbee asserts “architecture is a social art. And as a social art, it is our social responsibility to make sure we are delivering architecture that meets not only functional and creature comforts, but also spiritual comfort” [76]. Diebedo Francis Kere echoes Mockbee: “architecture is not just about building. It's a means of improving people's quality of life” [77].

One thing that is, however, common to all these quotes is that architecture is something other than just a building. Architecture, claimed Jay A. Pritzker “is intended to transcend the simple need for shelter and security by becoming an expression of artistry” [78]. In this context, a building is considered as no more than the sum of its parts. Architecture, however, is other than that. The whole takes on an independent existence from the parts it is made of, as an observer will perceive it as a distinct object from the objects it is composed of. If this is what the architects claim then how does the term, and mindset, transfer to edifices formed by non-humans? If architects and biologists are indeed concerned with developing interdisciplinary collaborations (to study, for example, ant nests), we need to dispel the notion of architecture being exclusive to humans and consider it from a non-anthropocentric perspective.

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3 Vitruvius (c.80-70 BC - c.15 BC), author of *De Architectura libri decem* (commonly referred to as “The  
4 Ten Books on Architecture”) [79], regarded as the first book on architectural theory, and often  
5 referred to as the first architect, asserted architecture to have three qualities: Firmitas, Utilitas and  
6 Venustas. Henry Wotton, a C17th translator, interpreted these terms as “firmness” (well  
7 constructed) and “commodity” (functional) for the first two, with Venustas being less well defined  
8 and often interpreted as “beauty” or “delight”. We take on the latter version on the premise that it  
9 implies something ephemeral and other than the sum of the parts, whilst beauty has connotations  
10 of the beholders eye and is tied to subjective concerns of taste and style. The first two concepts are  
11 unlikely to cause controversy between architects and biologists; both disciplines actually expresses  
12 them in similar terms as we will discuss below. Delight, however, will require more consideration on  
13 our part. Indeed aesthetics - which makes the whole “other” than the sum of its parts - is a concept  
14 difficult to operationalize in the scientific study of animal behavior, and we will attempt to find a  
15 middle-ground on which biologists and architects can build upon.  
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### 18 **3.1.1. Firmness**

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20 Vitruvius’ “firmness” is understood as the physical properties of a construction that guarantee its  
21 structural soundness, at the very least for the time the building is needed. These properties depend  
22 on trade-offs between many factors including construction material and methods, technological  
23 advances, substrate composition, environmental conditions, and costs. Architects use tools from  
24 physics, engineering and economics to balance these different factors and plan accordingly the  
25 construction process. Biologists use a similar set of tools to measure biological structures,  
26 characterize their construction process, and ultimately determine the balance of constraints made  
27 by the animals.  
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30 Architects and biologists are, for instance, equally interested in measuring the physical properties of  
31 construction material. Weight, density, strength and deformability are all determining factors in  
32 choosing construction material for buildings. Animals themselves are sensitive to the physical  
33 properties of the construction material. Termites, for example, preferentially dig through non-load-  
34 bearing over load-bearing wood, and build thicker load-bearing clay walls when attacking loaded  
35 wood [32]. Architects rely on tools from materials science and engineering to select materials with  
36 desirable physical properties, and from applied physics for combining these materials in a  
37 structurally sound manner. Software tools like Oasys’ GSA Building enables detailed analysis of  
38 structural solutions providing accurate prediction of material performance, how a structure interacts  
39 with the ground and the impact of footfall on irregular structures [80]. Autodesk’s Insight 360  
40 platform permits architects to simulate and analyse building energy and environmental performance  
41 so they can approach the design process with understanding of factors leading to better building  
42 performance outcomes throughout the building lifecycle [81]. Biologists rely on similar tools to  
43 quantify the physical properties of animal constructions. For instance, Cole et al. (2001) conducted a  
44 comparative study of the physical properties of nest paper in three species of wasps, showing that  
45 the fibre composition of the paper might explain differences in thickness and tensile strength  
46 between nests [26]. In termite mounds, King et al. (2015, 2017) used structural (e.g. mound  
47 geometry) and dynamic (e.g. air flow) measurements to demonstrate that a “simple combination of  
48 geometry, heterogeneous thermal mass, and porosity allows the mounds to use diurnal ambient  
49 temperature oscillations for ventilation” [82,83]. Finally, and somewhat bridging architecture and  
50 biology, the physical qualities of termite mound soil have inspired researchers to evaluate their use  
51 in human-made constructions, such as in compressed earth bricks [84] and pavement material [85].  
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3 This commonality of tools and approaches provides opportunities for direct interactions between  
4 biology and architecture. Indeed, the standardized language of physics and engineering is  
5 particularly useful to transfer “technology” between the two disciplines. Case in point, the passive  
6 ventilation system of termite mounds has inspired the design of several buildings [86], such as the  
7 Eastgate Centre in Harara, Zimbabwe for instance [87]. The study of the physical and mechanical  
8 properties of social insect constructions may therefore be the most obvious starting point for  
9 collaborations between architects and biologists, and the one that is most likely to generate direct  
10 applications of the building principles of natural systems.  
11

### 12 13 **3.1.2. Commodity** 14

15 Vitruvius’ “commodity” refers to the efficient organization of spaces and systems that support the  
16 functions of the construction. It determines how the different parts of the building are used by its  
17 occupants and the benefits that they receive from it, relative to other possible organizations of the  
18 building. This concept is critical to both human-constructions and biological structures, as it links  
19 form and function with each other. Unlike “firmness” which is studied with tools from physics and  
20 engineering mainly, “commodity” in architecture and biology is more often characterized with  
21 methods from behavior and psychology, with a particular interest in the interaction between the  
22 organization of the structure and the distribution of behaviors within.  
23

24 A first concern of both architects and biologists is the spatial separation of functions that might have  
25 an adverse effect on each other. An obvious example is the spatial segregation of feeding locations  
26 from excretory areas in order to reduce the spread of infections. In human-made buildings, this  
27 segregation is achieved by the physical separation of food storage, cooking and consumption areas  
28 from the lavatories. Segregation of function can also be enforced by social conventions and  
29 regulations that makes certain behaviors acceptable in some locations only (e.g. smoking bans inside  
30 publicly accessible buildings). Similarly the spatial separation of functions is also present in  
31 structures built by social insects (see Section 3.2.2).  
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34 Another common interest of architects and biologists is in determining how efficiently a structure is  
35 used, and how its organization balances different, often contradictory uses. In architecture, this can  
36 have important implications in terms of, for instance, building safety (e.g. during an evacuation) [88],  
37 economic consequences (e.g. time spent by customers in store aisles) [89], and access (e.g. to favor  
38 space use by certain categories of users). In social insect constructions, researchers more often look  
39 at issues of resource accessibility [17], information flow [90], and nest defensibility [91]. In any case,  
40 biologists and architects use here again similar tools to measure and predict the efficiency of a  
41 structure relative to one or more of these objectives. For instance, researchers and practitioners in  
42 both disciplines regularly employ agent-based model to determine how the spatial organization of a  
43 structure affects the distribution of individuals, be they ants in a network of galleries [92] or humans  
44 in an art gallery [63]. Fitting such models to data from human and non-human systems allows for  
45 direct comparison between them, as has been done multiple times in studies of building evacuation  
46 for instance [93–97].  
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49 Finally, tools from graph theory can be used to measure the efficiency of a structure in terms of  
50 connectivity between its different parts. It has been used to characterize structures built by social  
51 insects such as ant and termite nests [23,91], and ant foraging trails [17,18], but also human-made  
52 constructions such as urban settlements [71,98], communication networks [99], water distribution  
53 systems [100,101], and transportation networks [102]. More specifically graph theory has been  
54 applied in architectural design as a method of describing building form and a way of automatically  
55 generating plan arrangements [62,103]. For instance Space Syntax theory describes how connectivity  
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3 and integration of areas within buildings and cities epitomises human social relations, and through  
4 mapping the heterogeneity within architectural forms correlates topological relations between  
5 building and settlement configurations and people (see Hillier, 1996; Hillier & Hanson, 1986)  
6 [104,105]. Such approaches also allows for direct comparisons between human-made and insect-  
7 made networks that can be indicative of common building principles. For instance, Buhl et al. (2006)  
8 showed that street networks in non-planned settlements have similar cost-efficiency trade-offs as  
9 the emergent structure of ant tunnelling networks [98]. As in the previous section on “firmness” this  
10 commonality of tools and analysis language should allow for more frequent collaborations between  
11 architects and biologists.  
12

### 13 14 **3.1.3. Delight** 15

16 Finally, Vitruvius’ “Delight” is generally understood as an aesthetic quality, defined in terms of style,  
17 proportion or visual beauty, and is symptomatic of how architecture is a visually dominant discipline.  
18 That architecture is dominated by a concern for the visual is long held [106], and the visual sense has  
19 played a significant role in our evolution as a species. This emphasis has driven cultural and  
20 technological development; which has in turn reinforced the prominence of our visual sense (see  
21 Cairns 2017) [107]. But “delight” is not specifically attuned to the visual and there is a growing sense  
22 that architects should account for a wider sensorial domain in the artefacts they create [108,109].  
23 Indeed “delight” infers something of pleasure or joy, which is open to all sensation and sources of  
24 stimulation, and thus encompasses all senses.  
25

26  
27 If we follow the definition professed by Frederick Kiesler, that architecture is emotional, what  
28 distinguishes architecture from building is that the former evokes emotion [110]. Such a definition  
29 sidesteps the moral high ground of architectural practice and schools, because it states simply that  
30 architecture affects and causes emotion. Understanding architecture as such allows one (1) to  
31 transcend boundaries, because it relates to the sensing emotive capacity of the observer, and (2) to  
32 consider architecture a product of perceptual systems that perceive stimuli (see Gibson, 1966) [111].  
33

34 So, whether a construction, built by social insects or humans, can be considered architecture or not  
35 is open to interpretation. As such we are faced instead with philosophical traditions and how one  
36 sees the world, and thus one’s place amongst those things they share it with. We must ask then, if  
37 we are to accept the term “social insect architecture” whether ants, for example, have aesthetically-  
38 triggered emotions? We cannot sidestep this question.  
39

40  
41 While it is obvious that the nests of social insects have specialised functional dimensions [112–114],  
42 the question of whether they are also built aesthetically is difficult to address scientifically. There are  
43 no doubt that in the eyes of a human observer, social insect nests are beautiful objects [16].  
44 However, whether they are in the eyes of an ant or a honeybee is more complicated to answer.  
45 Social insects can react and associate meaning to a wide variety of stimuli [115–119], but whether  
46 they derive emotions from these stimuli is unknown - or at least undiscussed in the literature. Some  
47 species of social insects seem to be decorating their nests with artifacts which function is not  
48 immediately evident (e.g. the pebbles and twigs on meat ant nests [120]). But are these true  
49 aesthetic artifacts built with the intention of triggering emotions, or more simply construction  
50 patterns resulting from the evolutionary history of the organism, for instance as a mechanism for  
51 nest recognition? [120] And if the latter, doesn’t it apply as well to human artifacts? After all, our  
52 senses and cognitive processes are also the products of our evolutionary history, therefore our  
53 aesthetic experiences should be as well [121].  
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3 Taking a non-anthropocentric view we need to relinquish the idea that aesthetics is an intellectual  
4 pursuit, and that it may be a judgement (or act) based on the assignment of value to something. The  
5 concept of aesthetics was originally coined by the philosopher Alexander von Baumgarten (1741-  
6 1762), who argued aesthetics is the study of the plenitude and complexity of sensations [122] (also,  
7 *cf.* Gibson, 1966) [111]. When Kant took up the concept he drained it of its sensory plenitude,  
8 revising its significance to contemplation and judgement of beauty (see Howes and Classen 2013)  
9 [123]. If we take a step back (to Baumgarten) we may consider the edifices built by social insects,  
10 from the organism's perspective as having some aesthetic quality - whatever that might be. We may  
11 conclude then that architecture (in its widest sense) is a product of behaviours that support and  
12 enhance physiological and social needs. On the one side, to provide protection and shelter. On the  
13 other, to shape and manage activity. The former applies to all constructions by humans and animals.  
14 The latter to social organisms in particular (humans and most typically social insects), which use their  
15 constructions as a form of enabling device to organise actions and define social conditions [113,124].  
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18 Therefore we propose that what truly separates construction from architecture is that the reaction  
19 of an organism to the former cannot be distinguished from its reaction to a similar artifact resulting  
20 from extraneous processes (that is processes foreign to that organism). Architecture, on the  
21 contrary, carries a social information that has the potential of affecting the behavior of organisms  
22 beyond the simple physical constraints imposed by the organization of the structure on them. A  
23 builder assembles a construction, but makes it architecture by embedding messages in it - be they  
24 intentional to prompt or provoke behaviour or unintentional in which case they may be a by-product  
25 of the builders behaviour or happenstance.  
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### 28 **3.2. Construction as a way to shape space**

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30 One of the main outcomes of construction is - arguably - the organization of spatial relationships  
31 between individuals, their activities and their environment. Through construction organisms - be  
32 they humans or social insects - partition their environment into distinct zones that can support  
33 different functions (e.g. feeding vs excreting) and separate different habitats (e.g. outdoors vs  
34 indoors) or different populations (e.g. employees vs customers). This partitioning necessarily creates  
35 spatial relationships between the separated elements. This may seem obvious to the reader, yet the  
36 idea of space only appeared in architectural discourse in the late 19th Century, when it became  
37 important in two ways: first as the embodiment of human activity inside the architectural form [125]  
38 and second when it became aligned to aesthetic ideas in an attempt to define beauty [126]. The  
39 issue of space thereafter became a central topic in architecture, initially in terms of sensorial  
40 engagement with the environment [127]. (See van de Ven, 1987 for a concise history of how the  
41 idea of space has developed in architectural theory) [128].  
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44 The issue of space is also central to biology at all levels of biological organization. From the  
45 partitioning of biochemical reactions within cells [129] to the influence of large-scale environmental  
46 patterns on species distribution [130], measuring spatial relationships is critical to understanding life  
47 in general. In the context of this review, we are more specifically interested in how organisms  
48 reshape their environment through their building behaviour, and how in return the resulting  
49 constructions impose spatial constraints that direct further behaviours. These two questions apply  
50 similarly to humans and social insects, and the main goal of this section is therefore to identify  
51 research themes common to biologists and architects and to draw comparisons between their  
52 respective approaches.  
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3 For this purpose, we propose here that the spatial character of built constructions can be  
4 approached from three complementary and non-mutually exclusive angles. By no means do we  
5 claim that these angles are the only possible, but we think that they should encompass most of the  
6 research issues related to space and construction:  
7

- 8 1. First, we will consider that constructions almost always separate an outside from an inside  
9 world, most often for reasons linked to protecting the organisms from some aspects of their  
10 environment.
- 11 2. We will also discuss the role of the spatial organization of the construction and its  
12 interaction with behaviour in segregating functions within a population and in channeling  
13 the individuals' activities.
- 14 3. Finally, we will examine how the spatial configuration of the construction can itself generate  
15 functions that benefit the organisms without necessarily requiring their active participation.  
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### 18 **3.2.1. Constructions provide protection**

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20 The primary function of construction is arguably to provide shelter to organisms from adverse  
21 conditions in their environment. An enclosed, insulated space will for instance be less subject to  
22 climatic variations such as changes in temperature and humidity levels, thereby facilitating an  
23 organism's homeostatic regulation. Walls and ceilings also offer barriers that can shield - for a time  
24 at least - an organism from any physical threat, such as falling objects or predators. Therefore one of  
25 construction's most important purpose is to create a separation between an outside, often unsafe  
26 and unpredictable world, and an inside, more stable and less dangerous one.  
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29 Social insects are masters at building fortresses to protect their colonies from intruders. Their nests  
30 range from simple holes in the ground or in vegetation [131,132], to vast underground complexes of  
31 chambers interconnected by tunnels and housing sometimes several millions of individuals  
32 [133,134]. Like human strongholds, the nests of social insects are organized to limit outside access,  
33 with only a small number of entrances (often a single one). In many species, specialized workers -  
34 often called soldiers and morphologically distincts from the other workers - are found guarding  
35 these entrances against intruders [135,136]. In some species of ants and termites, these 'guards'  
36 have even evolved morphological and/or behavioral adaptations allowing them to plug the  
37 entrances with their own bodies, quickly preventing access to the inside of the nest when under  
38 attack [12,131,132,137,138]. Outside the fortress, several species of social insects also build  
39 protected passages that connect the nest to resources sometimes hundreds of meters away. These  
40 passages can be underground tunnels as in leaf-cutting ants and some termite species [133,139-  
41 141], mud tunnels (shelter tubes) built by termites along tree trunks [142,143], or even 'living' walls  
42 that *Dorylus* ants form along their trails out of their own bodies [144].  
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45 The nests of social insects are not built to resist physical threats only. Indeed many social insects  
46 species regulate the micro-climate within their nests in order to maintain stable living conditions,  
47 independent from variations of the outside environment [145]. Termite mounds are arguably the  
48 most striking examples of constructions by social insects capable of shielding the colony from  
49 changes in the external weather conditions [82,83,145-148]. The structure itself of the mound  
50 creates temperature gradients that in turn generates air currents, balancing the temperature within  
51 the nest and ensuring stable gas exchanges [82,83]. A similar phenomenon can be found in some  
52 leaf-cutting ant nests, which regulate the oxygen / carbon dioxide balance through passive air  
53 movements [35,149-152]. Social insects also regulate the internal conditions of the nest in a more  
54 active fashion. Bees, for instance, aggregate at the entrance of their hive on hot days and use their  
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3 wings to move hot air outside the hive and cooler air inside [153–155]. Army ants, which form  
4 temporary nests called bivouacs out of their own bodies, increase or decrease the spacing between  
5 each other to regulate the internal temperature of the colony [156,157]. Finally, in many ant species  
6 digging nests into the ground, the workers relocate regularly their brood away or toward the surface  
7 as it heats up or cools down, in order to maintain the brood near their optimal development  
8 temperature [158,159].  
9

10 Protection from the outside world comes at a cost for the colony. Evidently, the constant upkeep  
11 and remodeling of the nest structure takes away workers from other essential tasks such as foraging  
12 or taking care of the brood. A balance must therefore be found between maintaining the nests  
13 integrity and carrying on the other activities of the colony. It is evident that some species invest a lot  
14 of time and energy in building and maintaining their nests (e.g. African and Australian termite  
15 mounds; the vast underground nests of *Atta* ants) while others barely improve the pre-existing  
16 cavities in which they nest (e.g. rock ants and turtle ants). Do complex - and therefore costly to build  
17 and maintain - nests evolve only in species with a strong need for protection - against predators or  
18 the environment -, or is nest complexity secondary to evolving efficient behaviors to accomplish the  
19 other tasks necessary for the survival of the colony? To our knowledge, there has been no  
20 systematic study of this trade-off.  
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23 Like the ants, humans have long built structures for defence and protection from the climate. Both  
24 functions are fundamental form-generating forces in human architecture, but as architects have  
25 embraced advancements in technology the influence climate has on human construction has  
26 lessened. Similar to the strategies of ants described above, humans have occupied hollows in the  
27 ground, carved out underground buildings and networks, and capitalised on features of the  
28 landscape to regulate the micro-climate within dwellings and maintain stable living conditions.  
29 Dwellings built in the ground, such as the Matmata houses in the Sahara and the Opal miner's  
30 houses in Australia use a layer of earth as coolant, and Réso, a network of underground tunnels in  
31 Montreal provide protection during the long winter. In Naours, France, an underground settlement  
32 includes a bakery and chapel. In southern China the circular Tulou buildings are designed to offer  
33 protection from the monsoon rain, and in Normandy aerodynamic roofs provide protection from  
34 harsh Atlantic winds (See Piesik, 2017 for a review) [160].  
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36

37 Whilst societies have long constructed buildings using local materials and inherited construction  
38 techniques (vernacular architecture) to provide protection, innovation in the use of materials means  
39 the result is not simply a consequence of assembling gathered materials in a rudimentary way, but  
40 creatively transforming them. Ashanti huts, for example, have a wooden frame with a roof of  
41 branches on top, on which a layer of beaten mud is supported. Contrary to what you might expect  
42 the thick heavy walls don't support the roof, so structurally they act as curtain walls. This may be  
43 due to cultural influence, but it is also likely a result of climatic reasoning. An advantage of this  
44 construction is the phasing, providing shelter quickly while the walls are erected (see Rapoport,  
45 1969) [161].  
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48 Glass, is perhaps one the most important innovations in modern building, and has changed the way  
49 we perceive the difference between inside and outside space. It blurs the lines between the two by  
50 providing physical protection but visual connection. In turn this changes the way we behave and  
51 how we think about space. It is interesting to look back at how the issue of space arose in  
52 architectural discourse and came to inform the modernist ideal of how space is deemed to flow from  
53 one area to another. The conflation of inside and outside was central to the architectural ideology of  
54 Leberecht Migge (1881-1935), who promoted the interpenetration of architecture and landscape  
55 through rational geometric lines with extensive use of glass to connect the two. Glazed doors and  
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3 windows formed the *Zwischenglieder* (interstices) between inside and outside to provide connection  
4 with nature, and greenhouses encircling houses providing thermal protection in winter (see Haney,  
5 2011) [162]. Migge's interstitial notion of space does not compartmentalise and it does not follow  
6 the general tendency to categorise the world into discrete units: between internal and external, and  
7 for example rooms by function. This controlled and ordered categorisation transfers to how we  
8 perceive and consequently organise space. We will come back to this in the next section.  
9

### 10 11 **3.2.2. Organization**

12 Division of labor is a landmark of social life. Most social insects species are characterized by a strong  
13 behavioral, and also often physical differentiation between groups of individuals specialized in  
14 performing different tasks (e.g. foraging, brood tending, etc) inside the colony [163–166]. In many  
15 species, this division of labor is also characterized by the spatial segregation of tasks within the nest,  
16 with specialized areas dedicated to specific activities [163,167,168]. A typical example of this spatial  
17 organization of activities is the nest of leaf cutter *Atta* ants [20,133,134,169]. They are composed of  
18 a network of tunnels connecting chambers that are all dedicated to a specific task. Some chambers  
19 house fungus gardens that serve as primary food source for the colony. Others contain the brood at  
20 different stages of development. Finally, rubbish dumps are created inside and outside the nest,  
21 isolating the colony from the waste material it produces [170,171].  
22  
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24 The spatial segregation of tasks has important consequences on the organization of the colony.  
25 Indeed, it has been shown that interactions are much more frequent between ants performing  
26 similar tasks [168], and that interaction rates are important regulatory signals for activating and  
27 inhibiting workers to perform particular tasks [172–175]. Because activities are segregated within  
28 the nest, workers specializing on a particular set of tasks are therefore more likely to interact with  
29 other workers with a similar behavioral profile, increasing their ability to share relevant information  
30 about their preferred tasks. Moreover, as workers transition toward other behavioral profiles as  
31 they age, they might relocate progressively within the nest toward areas better suited to their new  
32 preferences, possibly helped by the rate of interactions with workers of the same or of different  
33 behavioral profiles.  
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36 It is interesting to note here that the spatial segregation of tasks is not necessarily accompanied by  
37 the building of barriers to physically separate them. In ants and honeybees for instance, the brood is  
38 often grouped by type (e.g. workers vs drones) or developmental stage within a single space,  
39 without walls separating them [30,176,177]. Similarly, the content of honeybee comb cells is often  
40 organized spatially, with brood-containing cells grouped together in the center of the comb,  
41 surrounded by a band of pollen-containing cells, and then a larger peripheral region of honey-  
42 containing cells, but again with no physical barrier between these different areas [30,178].  
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45 The existence of a spatial segregation of tasks without physical barriers is understood as the result of  
46 simple self-organizing processes of differential aggregation [177,179–181]. This suggests that  
47 different areas within a nest - with or without physical separation - might specialize in a particular  
48 type of task not because of their intrinsic characteristics, but because of social feedback loops  
49 between the workers: the more a task is performed at a location, the more likely it will be  
50 performed again at that location. For instance in a recent study, Czaczkes et al. (2015) showed that  
51 *Lasius* ants will preferentially drop their feces at specific locations within their nest (usually a specific  
52 corner of a specific chamber) [112], separate from other waste materials that are gathered in piles  
53 outside the nest (the 'trash') [112]. This behavior is most likely driven by social signals contained in  
54 the feces (e.g. pheromones) that stimulate ants to leave their feces where other ants have done it,  
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3 leading to the creation of - effectively - toilets. This self-organized spatial segregation of tasks [182–  
4 186] is at odd with the way it is achieved in human constructions. Indeed, buildings built by humans  
5 are planned ahead and each room is pre-assigned a type of task, and then fitted with all the required  
6 features for users to accomplish these tasks.  
7

8 The basic purpose of any building is to satisfy the physiological and social needs of the organism. On  
9 the one side, to provide protection and shelter; as discussed above. On the other, to shape and  
10 manage activity. The former transmits to all constructions: human and animal. The latter to social  
11 organisms (humans and most typically social insects), which build structures that act as a form of  
12 enabling device to organise activity and define social conditions. Scrutinizing built structures enables  
13 us to consider space retrospectively, as a system of social relations from which rules, or patterns, of  
14 inhabitation may be extrapolated. For instance, Bill Hillier and Julienne analysed the organization of  
15 built forms and illustrated how the configuration of space changes when specified from the  
16 perspective of each distinct area constituting planned arrangements [104]. Identifying the  
17 heterogeneity of built forms they revealed buildings to be systems of activity defined by the  
18 dynamics of social and cultural goings-on. Similarly, analysis of social insect nest structures illustrates  
19 intricate spatial arrangements and the social structure of the colony [91,187].  
21

22 Working out the organization of a building is one of the most important and taxing aspects of  
23 architectural design. The task of organising the numerous criteria of a building programme was  
24 identified by Horst Rittel and Melvin M. Weber as “wicked”, because planning problems tend to be  
25 combinatorially hard [188]. The typical approach to organising a building is to flatten the problem, so  
26 that the activities to be housed can be planned. This has led some, like Paul Coates (2010), to claim  
27 the way architects traditionally organise a building is most unnatural [66,189]. Inspired by the way  
28 natural systems are understood as pattern making and problem solving, architects are today looking  
29 to the replication of phenomena in biology and computer science (such as flocking [190], stigmergy  
30 [190–193], branching systems [193], food foraging and nest construction [194], replication  
31 [195,196], and so forth) as an alternative approach to modelling form and structure that evades the  
32 traditional top-down centralised decision making process of configuration. This has opened up a  
33 whole new way of thinking about configuration in architecture, which is bottom-up and generative,  
34 and reminds us of Migge’s interstitial notion of space whereby internal and external domains are  
35 conflated and flow into one another (see previous section).  
37

38 The architect Frederick Kiesler (1890-1965), who was strongly influenced by biology [61,197],  
39 promoted a notion of space extending Migge. He considered space to be continuous, or endless. Not  
40 in sense of the void but in terms of a line for which both ends meet. This notion of space, which is  
41 evident in both the organisation and materiality of his work (see Bognar 2003) [198], was informed  
42 but what he saw as a fundamental distinction between how humans construct and what he  
43 observed in nature. “Nature [,he says,] builds by cell division towards continuity whilst man can only  
44 build by joining together into a unique structure without continuity” [199]. His point being, humans  
45 construct through brute force (connecting parts together to form a whole: we bolt, glue and force  
46 elements together). In non-human constructions parts merge, overlap and conjoin one another as a  
47 consequence of self-organising and emergent processes. The concept of stigmergy describing social  
48 insect nest construction is a case in point, which we will come back to in Section 3.3.2. Kiesler sought  
49 to emphasise how we organise space and devise the arrangement of matter is tied to how we  
50 comprehend space and distinguish spatial relations.  
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### 3.2.3. Function building

An organism's fitness is not determined by its personal morphological, physiological and behavioral phenotypes only. It is also influenced by phenomena that result from its activity, but are not a physical part of its being [200]. This 'extended phenotype' includes structures built by the organism and that provide it with services increasing its survival and reproductive success. The nests of social insects colonies are exemplars of extended phenotypes that have played a critical role in their evolutionary history [201,202]. Besides providing protection (as discussed in Section 3.2.1) and a mean to organize the colony's activity (as discussed in Section 3.2.2), the architecture of the nest itself can generate other complex emergent functions for the benefit of the colony.

Perhaps the most well known example of a function that it 'outsourced' to the nest architecture by social insects is that of ventilation, permitting the regulation of temperature, humidity and respiratory gas composition within the nest [35,82,83,146,151,203–206]. This is a common occurrence in large ant and termite nests, which depth - and therefore insulation - could render air exchanges with the surface difficult in the absence of dedicated ventilation mechanisms. While ventilation can be actively performed by some social insects (e.g. in bees [145,153,155]), it is often achieved passively by nest structures that can harvest naturally-occurring physical phenomena. For instance, it was shown that the interaction between wind and nest structure - and in particular the orientation of nest openings relative to wind direction - was responsible for ventilation in the large nests of the leaf-cutting ant *Atta vollenweideri* [35,151,206]. A similar mechanism was found to be responsible for nest ventilation in the termite *Macrotermes michaelseni* [204]. In termites, the mound that covers the nest can also be built so that daily temperature fluctuations caused by the sun heating part of the mound generate convective flow driving the ventilation of the nest [82,83].

In all the examples above, the structure of the nest itself performs the function, independently from the behavior of the organisms that built it. In many cases however, the function of the structure only becomes apparent when in interaction with the behavior of the organism. For instance, topological and geometrical features of ants and termites networks of foraging trails and nest tunnels have been shown to guide the movement behavior of the workers [19,23,91,92,207–212], for instance facilitating the collective selection of the most efficient route within the network. In this case, the structure does not have a function by itself, but one is created when interacting with the behavior of the organisms.

Similarly, the structure of human constructions perform functions independently to provide and maintain suitable living conditions and support physiological and social needs. A classic example of the former is passive ventilation; termed "natural ventilation" to emphasise the lack of mechanical equipment to provide air exchange. The Eastgate Centre, mentioned earlier, is one example. Another is the Palace of Westminster's historic ventilation system designed in the 1840's by physician David Boswell Reid to serve the House of Commons and the House of Lords. These two debating chambers are internal spaces that have no external walls of their own. Reid's elaborate scheme includes more than 2,000 vertical shafts, smoke flues and ventilation channels, some up to 200m long, providing fresh air collected from towers and led through an intricate network to the basement of the building, where it was heated during winter, and released through outlets in the chambers. This included outlets placed in the seating, so fresh air was delivered directly to occupants [213].

More recently, Mesiniagra tower, designed by Ken Yeang, is a bio-climatic skyscraper in Malaysia, where the sun is a prime factor in design. Louvres provide protection from the sun, but Yeangs design was informed by the path of the sun, so the buildings form also acts as a shading device

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3 reducing solar gain [214]. The form and shape of buildings can also act as a device to distribute  
4 people and control the flow of movement. Crowd disasters are a prevailing issue [65,215,216] which  
5 has led to extensive data collection to investigate the dynamics of crowd behaviour [217,218]. Serial  
6 incidents at the Hajj, Mecca, has resulted in the reorganisation of the Hajj, and specifically a new  
7 design for the Jamarat bridge. Different levels serve pilgrims coming from different areas and  
8 directions to reduce crowding on the Jamarat plaza.  
9

10 Control is a fundamental factor of institutional buildings, which is clearly evident in Jeremy  
11 Bentham's Panopticon. His design is a system of control allowing observation of prison inmates by a  
12 single watchman, without the inmates being able to tell whether or not they are being watched. The  
13 building acts as a device to prevent, or reduce, the likelihood of undesirable behaviour [214,219]. On  
14 a grander scale, Haussmann's plan for Paris remodeled the city to modernise it and also provide  
15 physical control of the population. He replaced many narrow streets, which allowed the  
16 revolutionaries' to establish barricades, with broad boulevards and avenues. Less obviously, the  
17 wider streets function as a form of psychological crowd control – a mob may be less likely to revolt  
18 due to the expanse making them feel less powerful [220].  
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### 21 **3.3. Constructions as a way to shape information**

22  
23 All living systems communicate in some shape or form, be it through chemical emission (e.g. scent,  
24 pheromone), visual display (e.g. form, colour, movement), sound production (e.g. vocalisation,  
25 vibration) or electric currents, to inform others of their own state (e.g. mating status) or of the state  
26 of their environment (e.g. incoming danger) [221,222]. As hinted at in the previous section,  
27 communication can also be achieved through building. Indeed, each construction act, by modifying  
28 the content or configuration of the environment, has the potential of constraining or guiding future  
29 behaviours. In Batesonian epistemology, it is "a difference which makes a difference", that is an  
30 "elementary unit of information" [223]. If we accept that each feature of a construction potentially  
31 holds information - or even *is* information -, then we need to discuss the meaning of this concept in  
32 biology and architecture. In particular in this section, we will attempt to identify possible points of  
33 agreement and disagreement between the two fields in order to facilitate communication - no pun  
34 intended - and collaboration between researchers across the aisle.  
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38 The concept of information is rather proteiform in both the scientific and philosophical literature  
39 [224]. Scholars in all disciplines have already proposed an uncountable number of definitions of  
40 information. With this manuscript, it is neither our intent to introduce a new one, nor to discuss the  
41 relative merits of each existing definition. However in the following sections, we will often refer  
42 explicitly and implicitly to two of the most prominent definitions of information - that of Claude  
43 Shannon and that of Gregory Bateson - and we think it necessary to briefly describe and contrast  
44 them here.  
45

46 Claude Shannon's idea of information [225] is motivated by the need to measure and  
47 mathematically describe information in order to quantify differences between messages (e.g. to  
48 detect transmission errors) and degrees of dependence between different signals (e.g. to detect  
49 phase synchronization between separate sources of information). Rooted in statistics and probability  
50 theory, Shannon's information has been hugely influential in many disciplines in science and  
51 engineering because of the analytical tools it provides for measuring and comparing the information  
52 content of random variables independently of their meaning. As Gibson points out, Shannon's  
53 information excludes the meaning of a stimulus to focus on the quality of message transmission  
54 from source to receiver [111].  
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Gregory Bateson's ecological view of information is rooted in the cybernetic idea of communication and organisation. The elementary unit of information, he claims, is a difference that makes a difference. He states, a difference that makes a difference is an idea. It is a 'bit', a "unit" of information [223]. This somewhat paradoxical statement deserves unpacking. Whilst Shannon's concept of information is about reduction of uncertainty Bateson implies a process of distinction. Both imply an observer, making choices, but Bateson infers a system classifying inputs or sensations subsequent to the ability to discriminate, initially between self and other, between things [226]. He describes a referencing system that perceives and thereby distinguishes [227,228], and accounts for how entities, be they cells, organisms or agents in a computer model, engage with *their* world. Bateson's unit of information is thereby also a unit of survival, whereby a difference is a matter of trial and error through which habits emerge. His concept of information is the basis for a theory of learning.

With these two approaches of information in mind, we will examine three general areas concerned with construction and information:

1. First, we will examine biological communication and information, and in particular the concepts of cues and signals and how they provide some evolutionary context to the present discussion.
2. We will then consider the concept of stigmergy and how construction can shape social systems by embedding information in the environment.
3. Finally, we will discuss the importance of explicitness in the perception of information and how this might help explain fundamental differences between constructions in humans and social insects.

### 3.3.1. Cues, signals, and biological information

In the behavioural sciences, information generated by an organism is traditionally separated in two categories: cues and signals [221,222,229]. Signals are any information transferring features that have evolved specifically to convey information about the signaller or its environment to receivers. It is generally understood as resulting from the coevolution of emitting and receiving apparatuses, as well as associated behavioral responses. Signals are also often - though not always - associated with the notion of intentionality, that is the organism controls when and where to broadcast the signal.

On the other hand cues are features that can be used by an organism to guide its behaviour, but that were not evolved specifically to convey information between a signaller and receivers. Think for instance of a predator following the scent of a prey animal. The prey animal has not evolved its scent nor does it intentionally release it to inform the predator, yet the predator can evolve an apparatus to perceive the scent, as well as associated behavioral responses. If a cue provides an evolutionary advantage to the emitting organism (e.g. if it attracts potential mates), it can then be selected for and become a signal. However, while signals are intrinsically biological in nature (i.e. a product of evolution), cues can also be obtained from nonliving entities, like the position of the stars in the sky or the direction of the wind.

Cues and signals play an integral role in the construction behavior of social insects. For instance, the construction behavior of some ant and termite species have been shown to depend on environmental cues such as the strength and direction of air currents or the presence of physical heterogeneities in the landscape (see for instance Jost et al, 2007) [230]. These cues can influence both the initiation of the construction process (e.g. environmental heterogeneities serving as anchor points of constructions in ants, termites and wasps) [14,29,231] and the final result of the building

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3 activity (e.g. walls aligned along the direction of air currents in ants and termites) [230]. Signals, on  
4 the other hand, are more often associated with coordinating the actions of the individuals in the  
5 colony. For instance, the addition of pheromones to the construction material in ants and termites  
6 has arguably evolved to encourage individuals to add to structures built by nestmates rather than to  
7 random environmental heterogeneities [14]. It could also represent the freshness of the material,  
8 therefore indicating structures under construction requiring additional actions by workers.  
9

10 Similarly, environmental and contextual cues are fundamental factors influencing the building and  
11 formation of human constructions. Vernacular architecture perhaps best illustrates how  
12 determinants such as climate, availability of local construction materials, and the influence of local  
13 traditions has informed the design of human constructions. One of the most significant determinants  
14 is the climate (See section 3.2.1). Buildings in cold climates typically have few openings, windows are  
15 small or non-existent to prevent heat loss, and have high thermal mass or significant amounts of  
16 insulation. Conversely buildings in warm climates tend to be constructed of light materials to allow  
17 cross-ventilation through openings in the fabric of the building. The different aspects of human  
18 behaviour and environment has led to different building forms, evident in the variable contexts and  
19 cultures around the world [160,161,232]. Despite these variations all buildings are subject to the  
20 same laws of physics and hence demonstrate significant similarities, which are evident also in social  
21 insect constructions: see section 3.1.1.  
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24 However human constructions differ from that of insects in that they are also the product of socio-  
25 cultural factors that escape largely natural selection. As technology has advanced and human socio-  
26 culture has progressed with it, methods of construction have become more sophisticated and the  
27 form of buildings have evolved. Innovation and technological advancement allows architects to  
28 overcome constraints, such as those determining vernacular architecture. For example, the Gothic  
29 flying buttress was an innovation transferring gravitational forces to ground in a way that allowed  
30 walls to become lighter, which permitted greater expanses of glass and thereby daylight to flood a  
31 buildings interior. Applied to churches and cathedrals this technique of building provided a means to  
32 denote divinity and promote the authority of the church. So, human construction is not only  
33 informed by environmental/contextual information - like in social insects - but also enables cultural  
34 signs to be embedded in the construction itself. These signs develop through a process typically  
35 referred to as 'cultural evolution' [233–237], whereby knowledge, beliefs, languages, etc., are  
36 passed on from generation to generation (inheritance), modified over time, and may enter in  
37 competition with each other, leading to selection pressures not unlike that underlying natural  
38 selection.  
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### 43 **3.3.2. Stigmergy and spatial embedding of information**

44 The notion discussed above that construction - whether by humans or insects - embeds information,  
45 that is can influence future actions of the builders or the users is reminiscent of the concept of  
46 stigmergy in biology. This idea was first introduced by Pierre-Paul Grassé in 1959 to describe the  
47 construction behavior of termites [191,238]. Grassé explains that the organization of the building  
48 activity does not depend on direct coordination between the workers, but rather on indirect  
49 coordination achieved through the modification of the structure under construction. Each time a  
50 termite worker adds or remove material from the structure, it changes the configuration of the local  
51 environment around it. This change will influence subsequent building activities at or around its  
52 location, either by the same worker or other workers in the colony. Coordination at the colony level  
53 emerges from the repetition of such stigmergic processes, giving the impression that the colony is  
54 following some sort of well-defined plan.  
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3 Since Grasse's original insight, stigmergic coordination has been found to play a role in most  
4 constructions built by social insects. For instance, the primitively eusocial wasp *Polistes* builds its  
5 nest out of paper it produces by mixing its saliva with plant fibers [26]. This paper is then turned into  
6 walls that will ultimately form a comb of hexagonal cells. During the building of the comb, cells are  
7 not added randomly to the structure under construction: wasps are more likely to add new cells where  
8 existing cells already form three or more adjacent walls [13,239]. As a consequence of this  
9 preference, multiple wasps can coordinate their building activity and will first complete existing rows  
10 of cells in the comb before starting a new one. The result of this indirect coordination is a round  
11 shaped comb with approximately one hundred and fifty cells and, more importantly, without holes.  
12 Other examples of social insect construction relying on stigmergic coordination include internal and  
13 external structures of nests in ants and honey bees [14,178], trail networks in ants and termites  
14 [240–242], and cemeteries and refuse piles in ants [114,230].

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17 While it can be argued that stigmergy is a dominant organizational force in social insects  
18 construction, they also rely on other modes of coordination during building. In particular,  
19 environmental and social templates play an important role - often in combination with stigmergy - in  
20 determining the final shape of the construction [13,51]. For instance, *Macrotermes* termites adjust  
21 the size of their queen's chamber to match her size as she grows [243,244]. Similarly, rock ants  
22 (*Temnothorax albipennis*) adjust the size of their nest to the quantity of their brood [245–247]. In  
23 both cases, it is believed that volatile pheromones produced by the queen and the brood establish a  
24 chemical gradient around them that can be used as a template by the workers to determine the size  
25 of the construction. Environmental heterogeneities and gradients can also be used as templates by  
26 social insects, determining for instance the location at which a construction is initiated or its final  
27 orientation. Finally, social insects can use direct coordination to organize their building activity. This  
28 is the case for instance of the self-assemblages built by some species of ants (e.g. temporary nests,  
29 bridges, ladders) and bees (e.g. swarms, festoons) by attaching to each other [12,37,38,47,49]. While  
30 limited to a few species, these - quite literally - living architectures built through direct coordination  
31 have the advantage over stigmergic structures of being extremely plastic and reactive, sometimes  
32 assembling and disassembling in a matter of minutes or even seconds.

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36 As a concept to describe the coordinated building activity of social insects the concept of stigmergy  
37 does not, on first inspection, easily transfer to human society and its architecture. However, Grasse's  
38 idea of stigmergy can be extended to encompass all forms of cues and signals that organisms -  
39 including humans - leave in their environment that have the potential of mediating indirect  
40 interactions between individuals [51,191,192]. Stigmergic traces represent the information that  
41 organisms embed in the spatial context and, together with environmental influences, they define a  
42 large part of the information landscape accessible to each organism.

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45 In the social sciences, Grasse's original insight has been studied in the context of numerous forms of  
46 human activity, including the stock market, economies, traffic patterns, urban development and  
47 more besides [248–251]. One may claim even that the way architects design traditionally, through  
48 drawing sketches, is stigmergic; whereby a line drawn on the page breaks the homogeneity of the  
49 blank surface, and influences scribing the next line. Successive lines are added influenced by and  
50 influencing the developing pattern to mediate the development of an idea. Working in a team the  
51 same sketch is referred to and developed by others who are influenced by what they see and add to,  
52 adapt or emphasise aspects of the sketch. Building Information Modelling (BIM) uses a stored digital  
53 model, which is accessible to all members of a design team, who work on and develop the model in  
54 parallel, detecting clashes and developing the model collectively. Recently architects have begun  
55 experimenting with stigmergy literally as a method of generative design [252–257].

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3 As mentioned above (see section 3.2.2), the capacity to use the computer to simulate the autonomy,  
4 emergence, and distributed functioning of natural systems provides architects a new way of  
5 producing form and structure, and to think about the organisation of areas constituting a building or  
6 city. Adjacency and circulation are fundamental concerns in organising architectural layouts, because  
7 of factors like the movement of people, material and information between areas, and/or the need to  
8 control or supervise one area from another. The nature of such problems has been characterised as  
9 “wicked” [188] because of the interrelatedness of the factors involved. The food foraging behaviour  
10 of ants, for example, has been explored as an alternative method of organising distribution networks  
11 in buildings and cities. Instead of placing activity areas in relation to one another based on  
12 convention the stigmergic behaviour of assorted artificial ant colonies has been utilised as a method  
13 of self-aggregation, and applied to generating the desired arrangements between activities in a  
14 building [258], and to generate primitive room arrangements [255]. Poussepp proposed a model  
15 whereby circulation is developed as an emergent by-product of global morphogenesis of the built  
16 form [259], and proposed a tool for generating outline urban arrangements often associated with  
17 unplanned settlements [260]. The stigmergic behaviour evident in insect societies and animals has  
18 also been adopted as a method of form finding [253,257,261]. Carranza and Coates, for example,  
19 used the trails left behind by a population of swarming agents as a scaffold to wrap a continuous  
20 surface around [253].  
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24 Whilst stigmergy has been applied as an alternative approach to organising buildings and form  
25 finding, the casual form of urban aggregation evident in medieval villages, Brazillian favelas and  
26 Chinese Hutongs exemplifies stigmergic configuration driven by environmental constraints, as with  
27 vernacular architecture, but urban aggregation of this type is also driven by associations with one’s  
28 neighbour. Whilst cities are prone to top-down planning by the authorities they have been shown to  
29 operate as a dynamic, adaptive system based on interactions with neighbours, feedback and  
30 decentralised distribution of people, goods, information and energy [70,262,263]. Consequently  
31 urban growth has been evaluated computationally and illustrated to replicate natural systems  
32 [66,264]. Coates demonstrated how the formation of early human settlements is underpinned by  
33 geometrical constraints that inform the arrangement of unplanned as well and planned urban  
34 arrangements through a combination of environmental feedback and simple local rules [265]. The  
35 algorithmic approach driving contemporary architectural design today is motivated by this  
36 comprehension of geometrical rules and stigmergic behaviour of agent-systems evident in shaping  
37 urban settlements and the configuration of buildings. Coupled with the capacity of social insect  
38 societies to unscramble the wickedness of certain problems (like searching for food), architects are  
39 today looking to the decentralised and distributed control evident in the behaviour of social insects  
40 and how they form the structures they build [13,51,194].  
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### 44 **3.3.3. Explicit and implicit information**

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46 In the previous two sections, we discussed information from the point of view of the signaller:  
47 signals and cues are categorized based on whether the signaller has evolved them specifically to  
48 convey information about itself or its environment - or not (Section 3.3.1); and stigmergic traces are  
49 characterized by whether they persist in the environment even in the absence of the signaller  
50 (Section 3.3.2). In this section, we would like to shift the focus toward the receiver of the  
51 information. In particular, we would like to argue that information can influence the behavior of the  
52 receiver in either an explicit manner, or in an implicit one. We consider information as being explicit  
53 if the receiver has evolved - through natural or cultural evolution - perceptual and/or cognitive  
54 abilities to specifically give a meaning to this information. In other words, the organism has acquired  
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3 dedicated processes to operate on the content of a piece of information (e.g. neural pathways) and  
4 react to it accordingly. This corresponds to all forms of information for which the organisms  
5 possesses a receptor and mechanisms to interpret the output of the receptor.  
6

7 Implicit information, on the other hand, corresponds to features that can modify the behavior of an  
8 organism without requiring this organism to process or even perceive the associated stimuli. In other  
9 words, they are features of the physical and social environment that do not have a meaning for the  
10 organism - the organism might not even be able to perceive them -, yet they may influence its  
11 actions in a manner that the organism cannot control. These are often external physical forces  
12 applied on the organism without its knowledge (e.g. the tide pushing planktonic organisms toward  
13 the shore) [266] or barriers that constrain the movement of the organism. In some species of ants  
14 for instance, it was found that the geometry of their networks of foraging trails is asymmetrical:  
15 when a forager comes back toward its nest and reaches a branching point, the trail heading toward  
16 the nest after the branching point deviates less ( $\sim 30^\circ$ ) from the ant's original direction than the  
17 other trail ( $\sim 120^\circ$ ) which leads away from the nest [17,209,210,212,267]. While one species of ants  
18 may be able to use this information explicitly to navigate its trail network [210], others do not seem  
19 to perceive the difference and simply follow the path of 'least resistance' [92,209]. As a result, they  
20 are more likely to find their way back to the nest and their foraging output will be increased up to 3  
21 times, all this without requiring any navigational capabilities, spatial awareness or even the ability to  
22 detect the configuration of the branching point (as demonstrated using robots) [211].  
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25 Most studies on the building behavior and construction use of social insects involve characterizing  
26 explicit forms of information: pheromone deposits, tactile contacts, air movements, etc  
27 [14,230,268]. Few however have considered the importance of implicit information in shaping the  
28 collective behavior of the colony. Indeed one difficulty with studying implicit information, is that it is  
29 not always obvious to an external observer given the disconnection between this form of  
30 information and the sensory and cognitive apparatus of the organism. Yet, as in the example  
31 mentioned above, there is strong evidence that the topology and geometrical organization of the  
32 environment has an influence on the spatial distribution of organisms, even when they are  
33 imperceptible to said organisms. Therefore it should be explored more systematically in the context  
34 of social insect constructions.  
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37 Similarly, we can see examples of information that is embedded within the human built  
38 environment, and in architectural form, and how it too can have an influence on the behaviour of  
39 the perceiver. Again, this impact may be described as implicit or explicit. Winston Churchill's adage  
40 "we shape our buildings; thereafter they shape us" exemplifies the built environment a chief factor  
41 in determining behaviour. The correlation between perception of the environment and its implicit  
42 effects on well-being and behaviour has long interested psychologists [269]. The complexity of the  
43 built environment is a crucial factor contributing to human behaviour. Experiments measuring how  
44 the brain and body responds to different kinds of settings show people are bored and unhappy when  
45 faced with extensive bland facades, and by contrast, happy and stimulated by varied and permeable  
46 building frontages, which will in turn have an influence on where a person will choose to spend their  
47 time [270,271].  
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50 Quantitative theories and methods of analysing urban configurations, such as Space Syntax [272],  
51 illustrate the correlation between the geometrical composition of the built environment and social  
52 behaviour [104,105]. Graph based representations and statistical analysis of the structural  
53 properties of built form illustrates there is a direct correlation between the topology and  
54 geometrical organization of the environment and the spatial distribution of people and movement  
55 [273–275]. For example the least angular deviation along a route suggests the structure of the street  
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3 network is itself the key determinant of pedestrian flow. A pedestrian will tend to choose routes that  
4 require the least amount of turns, and this will correlate to their perception of how well integrated  
5 the street is within a network, and consequently to pedestrian density. The implication is that  
6 configuration can have effects on movement which are independent of attractors [276,277].  
7

8 The role of explicit information in the built environment is both more literal and more formalised.  
9 Road signs, and the demarcation of pathways is an obvious example. In extreme cases the function  
10 of the building is literally interpreted by the observer, such as “Big Duck”: a shop selling ducks and  
11 duck eggs that is built in the shape of a duck. However, a particular aspect that distinguishes the  
12 human use of information is our capacity to build arbitrary associations between things and to think  
13 metaphorically. Symbolism enables humans to communicate with other humans they don’t meet:  
14 i.e., symbols are an indirect form of communication, which are embedded and perceived throughout  
15 the built environment and have developed their associations (or meanings) through cultural  
16 evolution. A structure is symbolic when it acts as a vehicle of arbitrary content and the observer  
17 reads the embedded meaning, making architecture “other than” just a building: as discussed in  
18 section 3.1.3.  
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## 22 **4. Conclusion**

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24 Humans have long since looked on the natural world as a source of inspiration, and observation of  
25 what other animals can do has driven us to achieve feats beyond our natural capabilities; such as  
26 being able to fly. The idea of late that simple creatures build complex and dynamic constructions has  
27 spurred researchers to investigate the mechanisms behind such phenomena, from the building of  
28 social insects nests to the formation of cells, tissues, organs and ultimately organisms. The complex  
29 and coordinated behaviours resulting from interactions between individuals in a collective has led  
30 scientists and engineers to question how this understanding may be applied to human-related  
31 problems. Architects, on the other hand, who are becoming more aware of the parallels between  
32 biological processes and design, as well as the artefact making capacities of animals are turning  
33 more to biology to explore innovative methods of problem solving and designing.  
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36 Whilst there is a long history of biology influencing architectural endeavour only recently have  
37 biologists and architects begun to meet and collaborate. As indicated at the start of this paper this  
38 union brings inherent difficulties, as each discipline claims its own high ground and concepts  
39 fundamental to both are viewed distinctly from either side. Perhaps none more so than the concepts  
40 of “architecture”, “space” and “information”, which are not only fundamental to the sciences and  
41 humanities but everyday understanding. Consequently we set out in this review to cross-examine  
42 these concepts in biology and architecture and to establish a framework within which fundamentals  
43 that span both disciplines are apparent and beneficial to both, with the view to better enabling  
44 cooperation in the study of constructions built by social organisms and how these structures  
45 influence, direct and manage behaviour of social systems.  
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48 The primitive framework established here provides a basis on which to build. Having examined the  
49 notion of architecture we have proposed an open definition spanning human and non-human  
50 constructs, and reviewed the concepts of “space” and “information” in relation to human and social  
51 insect constructions. Additional concepts, such as “emotion”, may be scrutinised and included to  
52 facilitate and bolster interdisciplinary discourse. The notion of delight is perhaps beyond scientific  
53 reason but aesthetics (if we refer to Baumgarten [122,123]) may be considered a fundamental  
54 aspect of all living systems. The key, we suggest, is to analyse the occurrence of internal-external  
55 relations established by perceptual systems in the process of distinguishing information about their  
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3 world. The real issue is to avoid anthropomorphising the social insect and consider how the insect's  
4 perceptual system conveys information about its world. In so doing we should avoid seeking the  
5 meaning and establish the internal-external relations that inform, direct and lead to, for example,  
6 the termites pillar building activity.  
7

8 Living systems are embedded in their environment, which, we have proposed, from the organism's  
9 perspective is a matter of relations and forms that influence behaviour. These features, which may  
10 be evolved (signals) or not (cues), perceptible (explicit) or otherwise (implicit), constitute  
11 environmental pressures which constrain and coerce the activity of organisms. Spatial constraints  
12 are a fundamental feature of living systems, both in their development and in their unfolding  
13 engagement with the world [278,279]. Evident, for example, in the building of self-ventilating  
14 mounds in termites, the rules that govern construction can be seen as productive constraints,  
15 because they are sensed by the organism that responds to it, giving it a meaning, and ultimately  
16 creating a functional pattern (the mound and its passive ventilation) that improves the colony's  
17 fitness. It is a fundamental character of natural systems that spans scales from abiotic to social  
18 systems. This semiotic perspective unifies architecture and biology and, we hope, could be the basis  
19 for a more formal collaborative language between the two disciplines.  
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31

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