PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour

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Contents

Theme issue: Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour

	Article ID		Article ID
INTRODUCTION Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour N Pinter-Wollman, A Penn, G Theraulaz and SM Fiore	20170232	Exploring nest structures of acorn dwelling ants with X-ray microtomography and surface-based three-dimensional visibility graph analysis T Varoudis, AG Swenson, SD Kirkton and JS Waters The non-additive effects of body size on nest architecture in a polymorphic ant	20170237
ARTICLES		CL Kwapich, G Valentini and B Holidobler	20170235
Architecture, space and information in constructions built by humans and social insects: a conceptual review T Ireland and S Garnier	20170244	Visualizing aggregate movement in cities M Batty The impact of the 'open' workspace on human	20170236
The impact of the built environment on health behaviours and disease transmission in social systems		collaboration ES Bernstein and S Turban	20170239
N Pinter-Wollman, A Jelić and NM Wells The architecture of <i>network collective intelligence</i> : correlations between social network structure, spatial layout and prestine outcomes in an office	20170245	Predicting collective behaviour at the Hajj: place, space and the process of cooperation H Alnabulsi, J Drury and A Templeton	20170240
F Kabo	20170238	Can we identify general architectural principles that impact the collective behaviour of both human and	
Split between two worlds: automated sensing reveals links between above- and belowground social networks in a free-living mammal		animal systems? A Penn and JS Turner	20180253
JE Smith, DA Gamboa, JM Spencer, SJ Travenick, CA Ortiz, RD Hunter and A Sih	20170249		

PHILOSOPHICAL TRANSACTIONS B

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Introduction



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Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour

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Built structures, such as animal nests or buildings that humans occupy, serve two overarching purposes: shelter and a space where individuals interact. The former has dominated much of the discussion in the literature. But, as the study of collective behaviour expands, it is time to elucidate the role of the built environment in shaping collective outcomes. Collective behaviour in social animals emerges from interactions, and collective cognition in humans emerges from communication and coordination. These collective actions have vast economic implications in human societies and critical fitness consequences in animal systems. Despite the obvious influence of space on interactions, because spatial proximity is necessary for an interaction to occur, spatial constraints are rarely considered in studies of collective behaviour or collective cognition. An interdisciplinary exchange between behavioural ecologists, evolutionary biologists, cognitive scientists, social scientists, architects and engineers can facilitate a productive exchange of ideas, methods and theory that could lead us to uncover unifying principles and novel research approaches and questions in studies of animal and human collective behaviour. This article, along with those in this theme issue aims to formalize and catalyse this interdisciplinary exchange.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

Recently, multiple disciplines have separately begun to study how physical structures influence interactions among individuals and the emergent collective outcomes. For example, research in biology on social insects has begun to examine how nest architecture influences the collective behaviour of colonies [1]; research in social and cognitive sciences on humans has begun to investigate how buildings or environmental factors can alter social behaviour [2], collaboration [3] and other psychological factors [4]. Despite conceptual similarities among these fields, that is, theorizing on how the built environment may shape interactions and hence the resulting collective behaviours, there has been little, if any, interdisciplinary communication among these research communities. This theme issue brings these fields together to develop a new form of team science [5] and help shape future interdisciplinary research.¹ By bringing together a wide range of research disciplines and professions-from biology, physics, social science and architecture-we are better able to pose interdisciplinary questions and identify gaps to create interdisciplinary bridges. These articles illustrate how collaborative problem solving around complex scientific and societal problems can be advanced through teamwork [6]. Further, the methods and theories integrated in this theme issue point us towards

innovations that can advance our understanding of how to study these forms of complex collaborations (cf. [7]).

The contributions to this theme issue illustrate methodological advances, and implementation of methods to real-world problems through empirical studies and reviews of the literature. In this introduction, we first review methodological approaches from biology, physics and architecture to establish a common corpus of methods that will enable interdisciplinary work on the effects of the built environment on collective behaviour, as some of the papers in this theme issue have begun to do. We then outline the structure of the theme issue and highlight the findings of the contributed papers. To bring together the methodological approaches and insights from the contributed papers, we conclude with a set of general research questions for readers to consider. In service of developing an interdisciplinary science of architecture and collective behaviour, these questions are developed to prime thinking while readers review the multidisciplinary contributions in this issue.

2. Methodological approaches to study the effects of the built environment on collective behaviour

To study the impact of architecture on collective behaviour, it is necessary to quantify the built environment and the movement patterns inside these built structures that result in the interactions that underlie the emergence of collective behaviours. Here, we outline some of the methods used to obtain and describe these types of spatial and behavioural data and the quantitative approaches that have been used to analyse it.

(a) Quantifying structures

To determine the impact of the built environment on collective behaviours, one must first quantify the structure of the built environment. This task is not simple because there are many aspects of the environment that might be important to consider. First, physical structures span many scales. The smallest is the 'design scale', which refers to furniture, signs, etc. Next is the 'architectural scale', which refers to the arrangement of walls, doors, etc. The 'geographical scale' examines the arrangement of buildings, streets, etc. [8]. Second, there are multiple features that are part of the structure but are not simply geometric. For example, odours and acoustics can impact the way individuals interact [9]. Social insects relay on the odour of the chambers they occupy to determine what type of task is performed in them [10]. Acoustic signals, such as stridulating, can shape the way social insects move in their nest and structure them [11]. Noise can impact the communication between humans and odours in the environment may prevent or promote the use of certain areas in a building. Thus, an 'odour landscape' or an 'acoustic landscape' may be useful to quantify. For simplicity, we will focus our discussion here on quantifying the geometry and network topology of space. Although this focus on the configuration of space is a simplification, spatial patterns affect the perception of sound, sight and possibly odour, all important modes of communication for social communities.

(i) Extracting spatial attributes

Architects design the built environments that humans occupy, meaning that blueprints and other such representations (e.g. diagrams and sketches) can be used to capture the spatial attributes in the built environment. However, when examining the built structures that animals produce, there is no blue print with which to work. To address this, researchers are required to extract the spatial structure through 'reverse engineering'. The structure of nests that animals excavate can be extracted by pouring into the ground plaster, wax, various metals, such as zinc and aluminium [12], concrete and expanding foam [13]. These materials produce casts of the cavities that animals excavated, which can then be digitized or quantified manually. Another method for extracting the structure of nests is using a CT scanner [13-15]. The three-dimensional images produced by X-ray tomography allow the accurate measurement of the internal volumes of different structures in the nest, counting the number of chambers, and reconstruction of the communication network between chambers. Once the network of a structure has been extracted, the geometry and topology can be described and quantified, as discussed next.

(ii) Describing the geometry of space

The geometry of built structures has been quantified with a wide range of methods. Straightforward features such as distances, angles, areas or volumes of rooms and chambers, length of corridors in different locations or depths [13,16] provide a first glance at the geometry of space. However, these measures do not capture the global structure or the connectivity of the built environment, limiting the kinds of inferences that can be made about global architectural patterns. System-level quantification approaches, such as network theory and Space Syntax, provide descriptions of connectivity that go beyond the geometry of a single component, such as a room, in the built environment. Network theory has been used to describe both human- and animalmade structures to quantify connectivity [14], spatial overlap between occupants [2], structural robustness [1,17], number of junctions [18], etc. In network depiction of structures, corridors or tunnels are usually network edges and rooms or chambers are often the network nodes [1,2,18], but sometimes tunnel junctions are represented as network nodes [19,20]. Once a structure is represented as a network, one can use a wide range of network measures to quantify the structure and its properties [21]. Some of these measures include local connectivity (e.g. centrality of particular nodes or edges [22]), global connectivity (e.g. average degree of all nodes [18]), meshedness (the proportion of cycles in the network [20]), path overlap [2], accessibility (number of nodes in the network that can be reached in exactly h steps from a given node [22]) and others. A powerful method that has been used to quantify and study buildings designed by humans is Space Syntax. This is a theory of human society coupled to a set of methods for representing and quantifying the pattern properties of built space, first developed by Hillier & Hanson [23]. By representing patterns of connected space as networks and quantifying the properties of these networks, it has been possible to control the design variable in comparative studies of buildings and urban areas. Using these methods, it has been established that the configuration of the built environment is a primary determinant of patterns

of human movement [24], and the product of these patterns of movement in terms of co-presence in space and communication between people [25].

(b) Quantifying movements within structures

To uncover the way in which individuals interact within given structures, their movement and interaction patterns need to be tracked. There are many ways to track the movement patterns of humans and animals. Most commonly, such tracking is conducted through remote sensing either using tracking devices that are attached to the study subjects or with image analysis [26–29]. After movement patterns are extracted, they need to be analysed to gain insights about the behaviour of the individuals in the built environment, for instance, their spatial fidelity, identifying the patterns of interactions among individuals and the collective outcomes of these interactions and movements [30].

(i) Extracting movement patterns

Similarly to when quantifying structures, one first needs a description of movements before they can be analysed. In this case, there is more similarity between humans and animals because, in both cases, individuals can be tracked remotely and their movement patterns obtained. Both animals and humans can be tracked using devices that emit radio frequency. Human movements have been tracked by following cell phone signals or radio-frequency-based devices [31,32]. Similarly, the movement of ants has been tracked using RFID tags [27]. High-resolution movement patterns cannot always be achieved using such devices, so, more commonly, the type of information obtained from wearable devises is less granular. Such devices can be used to track interactions directly, through proximity detection in humans [32] and animals [33], and they can record movements in and out of certain spaces, such as stations of public transportation in human movements [8] and the movements of animals in and out of their nests [34,35].

Another common way to obtain the movement patterns of both humans and animals is image analysis. Machine vision algorithms have been developed to track humans [36-38], and animals (www.antracks.org, www.noldus. com) [39]. Some of these software can track unique individuals; however, that capacity is usually limited to small numbers or low densities of individuals. The main hurdle to tracking individuals over time is that, if they are not uniquely tagged, the identity of the trajectories will often switch when individuals interact. To allow for reliable long-term tracking of individuals in highly dense social environments, researchers have augmented image analysisbased strategies with unique identification tags. This includes tags such as colours [40] or QR codes (two-dimensional barcodes), which have now been deployed on ants [10,28,41], honeybees [42] and bumblebees [43]. Most of this work is confined to laboratory conditions. However, after validating tracking methods in the laboratory, those can be used in natural built structures.

(ii) Analysing trajectories

Once trajectories are extracted from movement data, there have been many ways to quantify them. Examining speed, turning patterns, distance travelled, etc., all require simple computations. Determining where, when and between whom, interactions occur is more complex [44]. Researchers often use proximity to determine if individuals interacted, however, that requires information about the study subject. For example, it is imperative to know how close two individuals need to be for an interaction to occur, how long they need to be in proximity for an interaction to be meaningful and whether other behaviours need to be accounted for. Furthermore, there could be different types of interactions. In social insects, brief antennal interactions, and longer trophallactic interactions, are used for different purposes and only a few automated image analysis software can distinguish between the two [42]. In human studies, tracking hardware may capture audio so that communication can be recorded, or, at least, documented (e.g. who is speaking and for how long) [32]. A behaviour that is often overlooked, but could be important, is stopping behaviour. For example, animals stopped at certain locations may facilitate high frequency of interactions [45]. The locations where animals tend to stop, or slow down, could be dictated by the built environment. This could be due to a narrow passage way [45,46] or, in the case of human structures, there could be some feature that leads people to gather, like a water cooler, where humans may discuss work [47].

In most situations, the interactions between individuals and their physical and social environment are tightly entangled. To connect a detailed quantitative description of individual-level interactions with the dynamics of motion observed at individual and group level, one has to adopt an incremental approach. Such an approach consists of first building a model, based on experiments, of the spontaneous motion of an isolated individual. The model is then used as a dynamical framework to include the effects of interactions of that individual with the physical environment and with neighbouring individuals [48]. The agreement between the model's predictions and experiments on several observables in different conditions and group sizes can then be used to validate the model [44].

(c) Linking the quantification of structures and movement

The true challenge we currently face is linking the quantification of structures and movements into one framework. First, the spatial scale of the built environment might be far greater than the spatial scale of the movements of each individual. For example, a single insect might have spatial fidelity to small regions of a large nest [43], so its movements will not be constrained by nest areas that it does not visit. One way around this challenge is by examining all the movements in aggregate, as done when using Space Syntax. Such aggregation has obvious trade-offs, such as not being able to identify how much each individual contributes to the complexity of the observed movements. Furthermore, as mentioned above, built structures have cues other than the physical attributes, such as odours and auditory cues that might impact the relationship between the built environment and the movements within it.

A powerful method for linking the structure of the built environment with the movement and interaction patterns of its occupants is conducting experimental manipulations. Both animals and humans can be studied in different, predetermined, structures and the structure attributes can be manipulated to make causative inference. In humans, such work can be done using virtual reality (VR), to reduce the costs of creating actual spaces [49]. The use of VR for such studies is still in its infancy and there is a need for measuring physiological responses and comparing those to situations of movement in the real world in structures that are identical to the simulated one [50,51].

Another way to link spatial and social networks is using a multilayer network framework [52]. In this framework, networks that link different types of nodes can be connected through interlayer edges and the complete system can be analysed in a single framework. This approach has been used to link different transportation modes. For example, including a layer for air transportation, a layer for train routes and a layer for roads in a multilayer network can facilitate the identification of efficient travel paths by considering the various transportation modes simultaneously [53]. Similarly, one can link a network of social interactions with a network of spatial positions. Edges in the social network will describe social relationships that facilitate collective behaviours, edges in the spatial network will link connected places and interlayer edges will link individuals to the locations where they spent time [52,54,55]. Such an approach is especially useful for large built structures in which each inhabitant occupies only a small part of the space.

3. Overview of contributed papers

This theme issue aggregates empirical studies and review articles that showcase the current state of the art and explore future potential research directions that bring together architecture and collective behaviour. We begin with a section on the effects of architecture on flow of information and disease, we continue with papers that showcase novel methods for advancing the quantification of both structures and the movements within them. Following are examples of how information gained from studies that combine a look at architecture and collective behaviour can be implemented to improve policy and future designs. We conclude this theme issue with a philosophical manuscript on the conceptual similarities and differences in the perception of architecture by humans and animals.

Built structures constrain the movements of the organisms inhabiting them, thus impacting the flow of information, ideas and disease. The way information is impacted by the built environment is discussed in this theme issue as a duet between an architect, Ireland, and a biologist, Garnier, in [56]. In their article, they re-examine the concepts of 'space' and 'information' to establish definitions spanning biology and architecture to enable cross-fertilization between these two disciplines. The authors discuss the informational content of constructions built by organisms and the influence these structures can have on the spatial and temporal organization of individual and collective behaviour. This idea is reminiscent of the concept of stigmergy introduced by Pierre-Paul Grassé in 1959 to describe the coordinated building mechanisms of termites [57]. However, Garnier & Ireland [56] stage their paper in the frame of thought of enactivism, which considers that cognition arises from a dynamic interaction between an acting organism and its environment [58-60]. In this respect, they make two important claims: (i) space is a fundamental form of information and (ii) it is necessary to adopt a semiotic perspective to analyse and

describe the influence of constructions on animal and human behaviour. In other words, it is necessary to take into account the way that different species perceive the space and extract information from it through their specific sensory interfaces, to better understand the impact of architecture on their behaviour.

By affecting the way individuals move and interact, the built environment can impact the spread of disease and information about health-promoting behaviours. The built environment can facilitate positive experiences, can increase longevity and promote healthy behaviours, reducing chronic disease. In a review of the literature, Pinter-Wollman et al. [61] discuss the ways in which the built environment can prevent and contain the chronic and infectious disease in both humans and wildlife. They take an interdisciplinary approach that melds perspectives from the fields of architecture, social science and biology. Interestingly, they find important parallels between the impact of built structure on humans and animals. For example, the materials that are chosen for building structures are often selected to promote hygiene. Furthermore, both humans and animals use the built environment to reduce interactions with sick individuals-either by quarantining them or by removing them from built structures. Differences between humans and animals include the idea that built structures may promote activity in humans to reduce chronic disease in humans. However, increasing activity can potentially decrease the lifespan of animals because activity might expose animals to dangers, such as predators. Therefore, built structures are used to protect certain individuals, such as ant queens, thus reducing their activity and increasing their lifespan.

These two review papers are followed by two empirical examples, one from humans and one from ground squirrels, of how the built environment can impact the flow of information and disease. In humans, Kabo [62] shows how characteristics of the built environment interact with social and organizational factors. His paper combines data on spatial proximity with survey questions on employee perceptions, to evaluate how both spatial proximity and social connections influence perceived prestige of team projects. He finds that spatial proximity correlates with social network structure and that this link impacts the perception of the prestige of the problem on which a team is working. This work points out how the centrality of an individual in a network can relate to cognition and collaboration via the access of individuals with high centrality to novel information. Further, centrality can be associated with one's physical location in an organizational setting. In particular, certain people may obtain their knowledge or status because they are located on the shortest route between other pairs of coworkers. Interestingly, less connected teams are considered to be working on more prestigious problems.

Ground squirrels are active both above- and belowground. Above-ground, squirrels forage for food and interact with each other with minimal physical constraints in their environment. However, in their extensive burrow system, interactions among colony members are restricted by the structure of their burrow. Using a novel tracking method, Smith *et al.* [63] uncover differences between the social networks that emerge above- and below-ground. These differences have important implications for how disease can be transferred between individuals, depending on whether its transmission is restricted to the burrow system (e.g. through microorganisms that live inside the soil) or if transmission is through contacts, in which case, transmission dynamics will differ above- and below-ground because of the different emergent social structures.

As noted, understanding collective behaviour and the built environment requires the quantification of structures, movements and the combination of the two. In this issue, Varoudis et al. [15] bring the first application, to our knowledge, of Space Syntax to the study of an animal structure. Traditionally used by architects and the study of human dwellings, here Space Syntax theory is used to describe the three-dimensional structures that are excavated by ants inside acorns. This synergy between architects and biologists has led to the advancement of two-dimensional methods used to study buildings of humans and expand it to the three-dimensional space that ants occupy. Ants are not constrained to walking on the floor (as humans are) and so understanding the layout of all surfaces and dimensions in their nests could prove important for uncovering their collective behaviour. The paper by Varoudis et al. [15] provides a methodological breakthrough for both the examination of structures built by animals and for the expansion of space syntax.

In addition to quantifying the topology of structures, one needs to quantify the movements that happen in them. Studies of transportation are ahead in this respect because human transportation has been studied for decades. Batty [8] provides a broad perspective on quantifying movement via examination of human transportation patterns in, and between, cities, and explains how to represent aggregated movements in cities. This is a necessary first step along the path to determining what impacts these movements and the interactions between the moving individuals, and in determining how space impacts these interactions. By providing visualization and analysis of movement patterns in physical space, Batty's work [8] opens up opportunities for further examination of the causes and consequences of these aggregate movements that could not be examined if the movements themselves were not quantifiable. Batty's work bridges between the geographical and architectural scales by focusing on the relationships between locations rather than on the role of each particular location. We are reminded that there are both temporal and spatial dynamics that need to be considered when quantifying movements, because movement patterns can change according to the scale on which they are observed. For example, a short time window of a day might result in very different movement patterns if weekdays are compared to weekends.

The study of the effects of architecture on collective behaviour would not be possible if structures were not built. In social insects, the building process is an emergent collective behaviour that has been studied extensively both empirically and using modelling [64-73]. In this theme issue, Kwapich et al. [19] show that the composition of the colony that is excavating a structure can substantially impact nest topology. In a polymorphic species of ant, Veromessor pergandei, smaller individuals build shorter and less complex nests than larger individuals. Most interestingly, mixed groups of both small and large individuals build nests that are larger and more complex than what would be expected by simply adding the behaviour of the small and large individuals. Thus, there are nonlinear effects that result in structures that one could not anticipate from simply adding the behaviour of the different types of individuals in the colony. Understanding how the occupants of the built environment impact its structure is a first step in uncovering the continuous feedback between built structures and the collective behaviour of the individuals that inhabit and build them.

Two studies in this theme issue study human interactions in diverse settings. Importantly, these studies link theory and methods from different disciplines to converge on a novel view of how collective behaviour is influenced by the context of interactions. Via a blend of social science theory and methods, along with electronic data and statistical modelling, these papers provide insights into how human interactions change due to the built environment.

Bernstein & Turban [32] cover a persistent debate in organizational theory about how spatial boundaries in offices influence collective behaviour and various organizational outcomes. Originally, social science theory suggested that open plan offices would increase contact between employees and improve social interactions. These improved social interactions would then improve organizational outcomesfrom the attitudinal (e.g. cohesion) to the behavioural (e.g. communication and information exchange). These organizational outcomes might then enhance collective intelligence that could be leveraged to improve organizational performance. The findings on open plan offices are mixed, with many studies finding a lack of employee satisfaction with these architectural design changes. In a unique study combining digital data of physical interactions with electronic communications, Bernstein & Turban [32] study what happens when organizations change from traditional workspace design to open office architectures. Across two separate studies, with different organizations, they find consistent results. By examining physical interactions and electronic communications simultaneously, they are able to uncover how a move to open offices counterintuitively decreases face-to-face interactions while increasing electronic interactions. Further, their data suggest that organizational productivity decreased with the move to an open office. This paper makes an important contribution by providing a robust methodology to continue research on how architectural designs influence collective behaviour.

With an innovative combination of theory and context, Alnabulsi et al. [74] study the annual Hajj to Mecca and examine how the built environment interacts with ritualistic behaviour and beliefs. Attended by millions of pilgrims, the Hajj is a unique setting for examining architecture and its influence on crowds. Through analyses of crowd density, coupled with survey methodology, Alnabulsi et al. [74] study collective behaviour through the lens of cooperative behaviour. They examine the psychological processes related to the social support experienced by pilgrims and uncover how identification with others determines the form of behaviour exhibited. Drawing from social identity theory, they interpret differences in providing social support when pilgrims are inside the Mosque area versus in the plaza. The differences in density between these two physical spaces, as well as differences in their ritualistic significance, illustrate how cultural aspects of the built environment can influence collective behaviour.

Last, Penn & Turner [75] provide interdisciplinary theorizing as a way to integrate many of the concepts across the biological, cognitive and social sciences. They draw from embodied and extended cognition theory, and integrate these with niche construction theory arising from the biological sciences. With this, they link developments in biomimetic architecture to identify general architectural principles. Their goal is to point the way forward to unifying research and theory across not only a variety of disciplines, but also across taxa and spatial scales.

4. A path forward

To guide thinking on the integration of concepts and methods, we provide below a set of general research questions and approaches to assist in the integration of research on the built environment, movement, interactions and collective behaviour. A recent issue of this journal presented many advances to the study of collective movement [76]. However, the study of collective movement often overlooks the impact of physical constraints. Rather, it focuses on the coordination of actions among individuals to produce collective movements. As seen in this theme issue, we propose that including a further examination of the effects of spatial constraints on collective actions, in particular the constraints imposed by the structures built by the organisms themselves (or other organisms), can add a novel, important, and often overlooked factor in determining the emergence of collective behaviour. As detailed above and seen in the articles in this theme issue, such an examination requires the quantification of structures, movements, and the combination of the two. In light of this, we offer research questions and approaches that provide a way to address these needs via interdisciplinary research.

First, the quantification of structures requires the development of innovations to extract spatial attributes as well as describe the geometry of spaces. To guide these ventures, one might consider identifying cross-disciplinary constructs and/ or methods that can be adapted to illuminate universals in structural design that influence collective behaviour. To quantify the various aspects of built structures, it might be fruitful to combine features of network theory with concepts from Space Syntax, to achieve a rich formulation of methods to quantify geometric features that influence collective behaviour.

Second, when considering the quantification of movements within structures, there is need to develop innovations for extracting movement patterns, analysing trajectories and linking these. Novel technological developments to track movement patterns continue to emerge, and working with engineers to implement and use new technologies can advance our understanding of how architecture influences collective behaviour. Furthermore, borrowing methods from movement ecology [76] and adapting them to smaller spatial scales with physical constraints can provide the tools necessary for quantifying movements.

Finally, the biggest challenge we anticipate is merging the examination of space and of movements into one framework to determine how these two interact to impact the emergence 6

of collective behaviours. For example, one can consider different scales of movements and ask how can complementary tracking techniques be expanded to integrate design-, architectural- and geographical-scales of the built environment. Such integration will allow the examination of how each level separately and/or all levels together impact movement patterns and collective behaviour. Cross-disciplinary methods may be used to disentangle the physical and social environment to advance theoretical understanding and empirical approaches for understanding how architecture influences collective behaviour. Finally, interdisciplinary research may develop a multi-modal and multi-sensory framework to capturing the varieties of signals communicated in different types of spaces, creating a link between the built environment and the behaviour of the occupants.

5. Conclusion

This theme issue, and the guiding research questions we offer, serves as an important foundation for a new line of interdisciplinary research on the effects of architecture on collective behaviour. By bringing together biologists, social scientists and architects, we expect to inspire new research questions and theoretical frameworks both within and across these disciplines. We hope that the exchange of methods, theory and concepts across disciplines seen in this theme issue will lead to novel scientific studies that cross traditional disciplinary boundaries.

Our hope is that the questions we raise, viewed in the light of the contributions of this theme issue, can be used to guide an interdisciplinary science of architecture and collective behaviour. Doing so can have far reaching scientific and practical implications. From the scientific standpoint, this can help us identify design universals in architecture that have evolved in the animal kingdom and may occur across species. From the practical standpoint, this can help us develop guidelines for novel designs of spaces that foster collective behaviour, enhance collaboration, and facilitate development of new forms of emergent cognition. Such innovative spaces can have substantial social and/or economic implications through the promotion of cohesion, creativity and effective teamwork.

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Endnote

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Review



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Architecture, space and information in constructions built by humans and social insects: a conceptual review

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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-fertilization 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.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

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 and 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 mould 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 tunnelling 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 accumulating material (e.g. wax, saliva-imbibed soil or vegetable fibres) that will form walls, pillars, floors and ceilings [14,26–35]. Finally, some ants and bees use their own bodies as construction

material, attaching to each other and creating dynamical structures such as bridges, ladders, holds and temporary nests [12,36–49].

The complexity and diversity of structures built by social insects is reminiscent of that of human beings [50]. Their construction rules are however radically different. Unlike human-made constructions that are most often composed of inert and standardized units assembled in a precise order, social insect constructions are built from more plastic and irregular components, and their assemblage results from distributed processes of self-organization with little to no supervision [13,51,52]. As a result, their structures are less standardized, but more capable of adjusting their conformation in response to changes in the conditions in which they are placed [12,37,38,53,54].

The parallels and divergences between the structures built by social insects and by humans have sparked a lot of interest in the architectural community [55-60]. The natural world has been an inspiration for architects since antiquity, with biology becoming a key influence on design thinking at the turn of the nineteenth century, when the analogical influence turned to interest in how biological systems develop and evolve [61,62]. Coupled with the computational capacity to simulate natural systems, architects are today exploring the self-organizing and emergent morphologies of biological phenomena to rethink how buildings and cities are designed [63-71]. The emergent, adaptable and situated structures built by social insects offer intriguing insights in particular for architects to re-evaluate not only the sustainable aspects of the human-built environment but also to question the distinction between cognitive phases of human architecture (i.e. between design, construction and occupancy stages) and to think about these as continuous. [72].

Recently, biologists and architects have started coming together to form a new community, interested in understanding the construction mechanisms used by social insects and their potential applications in human-made structures [55,73]. As is to be expected between two disciplines that have existed in parallel with little interaction, terminology has quickly become the first obstacle to creating a theoretical framework in which to ground the emerging field. During discussions preceding the writing of this manuscript, the authors have identified three concepts, in particular, that rendered their mutual understanding difficult: architecture, space and information. In what follows, we will first try to reconcile the somewhat liberal use by biologists of the concept of architecture with the more institutional definition that architects have of it. We will then discuss the concept of space in architecture and biology, and how social systems use space both as a source of information and a means to encode social information. Finally, we will discuss the idea of information itself and the effects of architecture on information flow and processing in social systems.

2. The scope of the review

One of the problems with interdisciplinary work is language, and is what may be termed the baggage individual disciplines bring to the table. Essentially, terminology can be a barrier for interdisciplinary exchange. Key terms, such as architecture, space and information have long conceptual histories, such that even their everyday use is awkward. Closer inspection only muddies the water further because of the way different disciplines claim the high ground with regards their specific outlook. 'Space', for example, is from one side an enclosure (i.e. it has boundaries) and from the other the void (i.e. the volume contained within these boundaries). Our capacity to mathematically articulate spatial scenarios gives the impression that '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, the statutory body for the registration of architects in the UK, protect the term in law. Yet, these terms (architecture and architect) are often borrowed to refer to complicated structures and artefacts, such as software applications and circuit boards, recognized 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 that 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-fertilization between disciplines, working in the areas of collective behaviour and analysis of the structures and edifices constructed by nonhumans; and to facilitate how this area of study may better contribute to the field of architecture.

3. Towards an interdisciplinary framework

(a) 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 in 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' (see Hales 2005 [77]).

One thing that is, however, common to all these quotes is that architecture is something other than just a building. Jay A. Pritzker claimed that architecture '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 is perceived to have an independence distinct from the objects it is composed of. If this is what the architects claim then how do 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.

Vitruvius (ca 80-70 BC to ca 15 BC) wrote De Architectura libri decem (commonly referred to as 'The Ten Books on Architecture' [79]), which is regarded as the first book on architectural theory. Often referred to as the first architect, he asserted architecture to have three qualities: Firmitas, Utilitas and Venustas. Henry Wotton, a seventeenth century translator, interpreted these terms as 'firmness' (well-constructed) and 'commodity' (functional) for the first two, with Venustas being less well defined and often interpreted as 'beauty' or 'delight'. We take on the latter version on the premise that it implies something ephemeral and other than the sum of the parts, while beauty has connotations of the beholder's eye and is tied to subjective concerns of taste and style. The first two concepts are unlikely to cause controversy between architects and biologists; both disciplines actually express them in similar terms, as we will discuss below. Delight, however, will require more consideration on our part. Indeed aesthetics-which makes the whole 'other' than the sum of its parts-is a concept difficult to operationalize in the scientific study of animal behaviour, and we will attempt to find a middle-ground that biologists and architects can build upon.

(i) Firmness

Vitrivius' 'firmness' is understood as the physical properties of a construction that guarantee its structural soundness, at the very least for the time the building is needed. These properties depend on trade-offs between many factors including construction material and methods, technological advances, substrate composition, environmental conditions and costs. Architects use tools from physics, engineering and economics to balance these different factors and plan accordingly the construction process. Biologists use a similar set of tools to measure biological structures, characterize their construction process and ultimately determine the balance of constraints made by the animals.

Architects and biologists are, for instance, equally interested in measuring the physical properties of construction material. Weight, density, strength and deformability are all determining factors in choosing construction material for buildings. Animals themselves are sensitive to the physical properties of the construction material. Termites, for example, preferentially dig through non-load-bearing over load-bearing wood, and build thicker load-bearing clay walls when attacking loaded wood [32]. Architects rely on tools from materials science and engineering to select materials with desirable physical properties, and from applied physics for combining these materials in a structurally sound manner. Software tools like Oasys' GSA Building (see https://www.oasyssoftware.com/products/ structural/gsa-building/) enables detailed analysis of structural solutions providing an accurate prediction of material performance, how a structure interacts with the ground and the impact of footfall on irregular structures. Autodesk's Insight 360 platform (see https://insight360.autodesk.com/oneenergy) permits architects to simulate and analyse building energy and environmental performance so they can approach the design process with the understanding of factors leading to better building performance outcomes throughout the building life cycle [80]. Biologists rely on similar tools to quantify the physical properties of animal constructions. For instance, Cole et al. [26] conducted a comparative study of the physical properties of nest paper in three species of wasps, showing that the fibre composition of the paper might explain differences in thickness and tensile strength between nests. In termite mounds, King et al. [81,82] used structural (e.g. mound geometry) and dynamic (e.g. air flow) measurements to demonstrate that a 'simple combination of geometry, heterogeneous thermal mass, and porosity allows the mounds to use diurnal ambient temperature oscillations for ventilation' ([82], p.11589). Finally, and somewhat bridging architecture and biology, the physical qualities of termite mound soil have inspired researchers to evaluate their use in human-made constructions, such as in compressed earth bricks [83] and pavement material [84].

This commonality of tools and approaches provides opportunities for direct interactions between biology and architecture. Indeed, the standardized language of physics and engineering is particularly useful to transfer 'technology' between the two disciplines. Case in point, the passive ventilation system of termite mounds has inspired the design of several buildings [85], such as the Eastgate Centre in Harara, Zimbabwe, for instance [86]. The study of the physical and mechanical properties of social insect constructions may, therefore, be the most obvious starting point for collaborations between architects and biologists, and the one that is most likely to generate direct applications of the building principles of natural systems.

(ii) Commodity

Vitrivius' 'commodity' refers to the efficient organization of spaces and systems that support the functions of the construction. It determines how the different parts of the building are used by its occupants and the benefits that they receive from it, relative to other possible organizations of the building. This concept is critical to both human constructions and biological structures, as it links form and function with each other. Unlike 'firmness', which is mainly studied with tools from physics and engineering, 'commodity' in architecture and biology is more often characterized with methods from behaviour and psychology, with a particular interest in the interaction between the organization of the structure and the distribution of behaviours within.

A first concern of both architects and biologists is the spatial separation of functions that might have an adverse effect on each other. An obvious example is the spatial segregation of feeding locations from excretory areas in order to reduce the spread of infections. In human-made buildings, this segregation is achieved by the physical separation of food storage, cooking and consumption areas from the lavatories. Segregation of function can also be enforced by social conventions and regulations that make certain behaviours acceptable in some locations only (e.g. smoking bans inside publicly accessible buildings). Similarly, the spatial separation of functions is also present in structures built by social insects (see §3b(ii)).

Another common interest of architects and biologists is in determining how efficiently a structure is used, and how its organization balances different, often contradictory uses. In architecture, this can have important implications in terms of, for instance, building safety (e.g. during an evacuation) [87], economic consequences (e.g. time spent by customers in store aisles) [88] and access (e.g. to favour space use by certain categories of users). In social insect constructions, researchers more often look at issues of resource accessibility [17], information flow [89] and nest defensibility [90]. In any case, biologists and architects again use similar tools here to measure and predict the efficiency of a structure relative to one or more of these objectives. For instance, researchers and practitioners in both disciplines regularly employ agent-based models to determine how the spatial organization of a structure affects the distribution of individuals, be they ants in a network of galleries [91] or humans in an art gallery [63]. Fitting such models to data from human and non-human systems allows for direct comparison between them, as has been done multiple times in studies of building evacuation, for instance [92–96].

Finally, tools from graph theory can be used to measure the efficiency of a structure in terms of connectivity between its different parts. The tools have been used to characterize structures built by social insects such as ant and termite nests [23,90], and ant foraging trails [17,18], but also human-made constructions such as urban settlements [71,97], communication networks [98], water distribution systems [99,100] and transportation networks [101]. More specifically, graph theory has been applied in architectural design as a method of describing building form and a way of automatically generating plan arrangements [62,102]. For instance, Space Syntax theory describes how connectivity and integration of areas within buildings and cities epitomize human social relations, and through mapping, the heterogeneity within architectural forms correlates topological relationships between building and settlement configurations and people [103,104]. Such approaches also allow for direct comparisons between human-made and insect-made networks that can be indicative of common building principles. For instance, Buhl et al. [97] showed that street networks in non-planned settlements have similar cost-efficiency trade-offs to the emergent structure of ant tunnelling networks. As in the previous section on 'firmness', this commonality of tools and analysis language should allow for more frequent collaborations between architects and biologists.

(iii) Delight

Finally, Vitrivius' 'Delight' is generally understood as an aesthetic quality, defined in terms of style, proportion or visual beauty, and is symptomatic of how architecture is a visually dominant discipline. That architecture is dominated by a concern for the visual is long held [105], and the visual sense has played a significant role in our evolution as a species. This emphasis has driven cultural and technological development, which has in turn reinforced the prominence of our visual sense [106]. But 'delight' is not specifically attuned to the visual and there is a growing sense that architects should account for a wider sensorial domain in the artefacts they create [107,108]. Indeed 'delight' infers something of pleasure or joy, which is open to all sensation and sources of stimulation, and thus encompasses all senses.

If we follow the definition professed by Frederick Kiesler, that architecture is emotional, what distinguishes architecture from the building is that the former evokes emotion [109]. Such a definition sidesteps the moral high ground of architectural practice and schools, because it states simply that architecture affects and causes emotion. Understanding architecture as such allows one (i) to transcend boundaries, because it relates to the sensing emotive capacity of the observer and (ii) to consider architecture a product of perceptual systems that perceive stimuli [110].

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

While it is obvious that the nests of social insects have specialized functional dimensions [111-113], the question of whether they are also built aesthetically is difficult to address scientifically. There is no doubt that in the eyes of a human observer, social insect nests are beautiful objects [16]. However, whether they are in the eyes of an ant or a honeybee is more complicated to answer. Social insects can react and associate meaning to a wide variety of stimuli [114-118], but whether they derive emotions from these stimuli is unknown-or at least undiscussed in the literature. Some species of social insects seem to be decorating their nests with artefacts whose function is not immediately evident (e.g. the pebbles and twigs on meat ant nests [119]). But are these true aesthetic artefacts built with the intention of triggering emotions, or more simply construction patterns resulting from the evolutionary history of the organism, for instance, as a mechanism for nest recognition? [119]. If the latter, does this not apply to human artefacts as well? After all, our senses and cognitive processes are also the products of our evolutionary history, therefore our aesthetic experiences should be as well [120].

Taking a non-anthropocentric view, we need to relinquish the idea that aesthetics is an intellectual pursuit, and that it may be a judgement (or act) based on the assignment of value to something. The concept of aesthetics was originally coined by the philosopher Alexander von Baumgarten (1741-1762), who argued aesthetics is the study of the plenitude and complexity of sensations [121] (also, cf. [110]). When Kant took up the concept he drained it of its sensory plenitude, revising its significance to contemplation and judgement of beauty (see Howes & Classen 2013 [122]). If we take a step back (to Baumgarten), we may consider the edifices built by social insects, as having some aesthetic quality from the organism's perspective-whatever that might be. We may conclude then that architecture (in its widest sense) is a product of behaviours that support and enhance physiological and social needs. On the one side, to provide protection and shelter and on the other, to shape and manage activity. The former applies to all constructions by humans and animals, the latter to social organisms in particular (humans and most typically social insects) that use their constructions as a form of enabling the device to organize actions and define social conditions [112,123].

Therefore, we propose that what truly separates construction from architecture is that the reaction of an organism to the former cannot be distinguished from its reaction to a similar artefact resulting from extraneous processes (that is, processes foreign to that organism). Architecture, on the contrary, carries social information that has the potential of affecting the behaviour of organisms beyond the simple physical constraints imposed by the organization of the structure on them. A builder assembles a construction, but makes it architecture by embedding messages in it—be they intentional to prompt or provoke behaviour or unintentional, in which case they may be a by-product of the builders' behaviour or happenstance.

(b) Construction as a way to shape space

One of the main outcomes of construction is, arguably, the organization of spatial relationships between individuals, their activities and their environment. Through construction, organisms-be they humans or social insects-partition their environment into distinct zones that can support different functions (e.g. feeding versus excreting) and separate different habitats (e.g. outdoors versus indoors) or different populations (e.g. employees versus customers). This partitioning necessarily creates spatial relationships between the separated elements. This may seem obvious to the reader, yet the idea of space only appeared in architectural discourse in the late nineteenth century, when it became important in two ways: first as the embodiment of human activity inside the architectural form [124], and second when it became aligned to aesthetic ideas in an attempt to define beauty [125]. The issue of space thereafter became a central topic in architecture, initially in terms of sensorial engagement with the environment [126]. (See van de Ven [127] for a concise history of how the idea of space has developed in architectural theory.)

The issue of space is also central to biology at all levels of biological organization. From the partitioning of biochemical reactions within cells [128] to the influence of large-scale environmental patterns on species distribution [129], measuring spatial relationships is critical to understanding life in general. In the context of this review, we are more specifically interested in how organisms reshape their environment through their building behaviour, and how in return the resulting constructions impose spatial constraints that direct further behaviours. These two questions apply similarly to humans and social insects, and the main goal of this section is, therefore, to identify research themes common to biologists and architects and to draw comparisons between their respective approaches.

For this purpose, we propose here that the spatial character of built constructions can be approached from three complementary and non-mutually exclusive angles. By no means do we claim that these angles are the only possible, but we think that they should encompass most of the research issues related to space and construction:

- 1. First, we will consider that constructions almost always separate an outside from an inside world, most often for reasons linked to protecting the organisms from some aspects of their environment.
- 2. We will also discuss the role of the spatial organization of the construction and its interaction with behaviour in

segregating functions within a population and in channelling the individuals' activities.

3. Finally, we will examine how the spatial configuration of the construction can itself generate functions that benefit the organisms without necessarily requiring their active participation.

(i) Constructions provide protection

The primary function of construction is arguably to provide shelter to organisms from adverse conditions in their environment. An enclosed, insulated space will, for instance, be less subject to climatic variations such as changes in temperature and humidity levels, thereby facilitating an organism's homeostatic regulation. Walls and ceilings also offer barriers that can shield—for a time at least—an organism from any physical threat, such as falling objects or predators. Therefore, one of construction's most important purposes is to create a separation between an outside, often unsafe and unpredictable world, and an inside, more stable and less dangerous one.

Social insects are masters at building fortresses to protect their colonies from intruders. Their nests range from simple holes in the ground or in vegetation [130,131], to vast underground complexes of chambers interconnected by tunnels and housing sometimes several millions of individuals [132,133]. Like human strongholds, the nests of social insects are organized to limit outside access, with only a small number of entrances (often a single one). In many species, specialized workers-often called soldiers and morphologically distincts from the other workers-are found guarding these entrances against intruders [134,135]. In some species of ants and termites, these 'guards' have even evolved morphological and/or behavioural adaptations allowing them to plug the entrances with their own bodies, quickly preventing access to the inside of the nest when under attack [12,130,131,136,137]. Outside the fortress, several species of social insects also build protected passages that connect the nest to resources sometimes hundreds of metres away. These passages can be underground tunnels as in leaf-cutting ants and some termite species [132,138-140], mud tunnels (shelter tubes) built by termites along tree trunks [141,142], or even 'living' walls that Dorylus ants form along with their trails out of their own bodies [143].

The nests of social insects are not built to resist physical threats only. Indeed many social insect species regulate the micro-climate within their nests in order to maintain stable living conditions, independent from variations of the outside environment [144]. Termite mounds are arguably the most striking examples of constructions by social insects capable of shielding the colony from changes in the external weather conditions [81,82,144-146]. The structure itself of the mound creates temperature gradients that, in turn, generate air currents, balancing the temperature within the nest and ensuring stable gas exchanges [81,82]. A similar phenomenon can be found in some leaf-cutting ant nests, which regulate the oxygen/carbon dioxide balance through passive air movements [35,147-150]. Social insects also regulate the internal conditions of the nest in a more active fashion. Bees, for instance, aggregate at the entrance of their hive on hot days and use their wings to move hot air outside the hive and cooler air inside [151–153]. Army ants, which form temporary nests called bivouacs out of their own bodies, increase or

decrease the spacing between each other to regulate the internal temperature of the colony [154]. Finally, in many ant species digging nests into the ground, the workers regularly relocate their brood away from or towards the surface as it heats up or cools down, in order to maintain the brood near their optimal development temperature [155,156].

Protection from the outside world comes at a cost for the colony. Evidently, the constant upkeep and remodelling of the nest structure takes away workers from other essential tasks such as foraging or taking care of the brood. A balance must, therefore, be found between maintaining the nest's integrity and carrying on the other activities of the colony. It is evident that some species invest a lot of time and energy in building and maintaining their nests (e.g. African and Australian termite mounds; the vast underground nests of Atta ants), while others barely improve the pre-existing cavities in which they nest (e.g. rock ants and turtle ants). Do complex-and therefore costly to build and maintainnests evolve only in species with a strong need for protection-against predators or the environment-or is nest complexity secondary to evolving efficient behaviours to accomplish the other tasks necessary for the survival of the colony? To the best of our knowledge, there has been no systematic study of this trade-off.

Like the ants, humans have long built structures for defence and protection from the climate. Both functions are fundamental form-generating forces in human architecture, but as architects have embraced advancements in technology the influence climate has on human construction has lessened. Similar to the strategies of ants described above, humans have occupied hollows in the ground, carved out underground buildings and networks, and capitalized on features of the landscape to regulate the micro-climate within dwellings and maintain stable living conditions. Dwellings built in the ground, such as the Matmata houses in the Sahara and the Opal miners' houses in Australia use a layer of the Earth as coolant, and Réso, a network of underground tunnels in Montreal provide protection during the long winter. In Naours, France, an underground settlement includes a bakery and chapel. In southern China, the circular Tulou buildings are designed to offer protection from the monsoon rain, and in Normandy aerodynamic roofs provide protection from harsh Atlantic winds (see Piesik [157] for a review).

While societies have long constructed buildings using local materials and inherited construction techniques (vernacular architecture) to provide protection, innovation in the use of materials means the result is not simply a consequence of assembling gathered materials in a rudimentary way, but creatively transforming them. Ashanti huts, for example, have a wooden frame with a roof of branches on top, on which a layer of beaten mud is supported. Contrary to what you might expect, the thick heavy walls do not support the roof, so structurally they act as curtain walls. This may be due to cultural influence, but it is also likely a result of climatic reasoning. An advantage of this construction is the phasing, providing shelter quickly while the walls are erected [158].

Glass is perhaps one the most important innovations in modern building, and has changed the way we perceive the difference between inside and outside space. It blurs the lines between the two by providing physical protection but visual connection. In turn this changes the way we behave and how we think about space. It is interesting to look back at how the issue of space arose in architectural discourse and came to inform the modernist ideal of how space is deemed to flow from one area to another. The conflation of inside and outside was central to the architectural ideology of Leberecht Migge (1881-1935), who promoted the interpenetration of architecture and landscape through rational geometric lines with extensive use of glass to connect the two. Glazed doors and windows formed the Zwischenglieder (interstices) between inside and outside to provide connection with nature, and greenhouses encircling houses providing thermal protection in winter [159]). Migge's interstitial notion of space does not compartmentalize and it does not follow the general tendency to categorize the world into discrete units: between internal and external, and, for example, rooms by function. This controlled and ordered categorization transfers to how we perceive and consequently organize space. We will come back to this in the next section.

(ii) Organization

Division of labour is a landmark of social life. Most social insect species are characterized by a strong behavioural, and also often physical differentiation between groups of individuals specialized in performing different tasks (e.g. foraging, brood tending, etc.) inside the colony [160-163]. In many species, this division of labour is also characterized by the spatial segregation of tasks within the nest, with specialized areas dedicated to specific activities [160,164,165]. A typical example of this spatial organization of activities is the nest of leaf cutter Atta ants [20,132,133,166]. They are composed of a network of tunnels connecting chambers that are all dedicated to a specific task. Some chambers house fungus gardens that serve as primary food source for the colony. Others contain the brood at different stages of development. Finally, rubbish dumps are created inside and outside the nest, isolating the colony from the waste material it produces [167,168].

The spatial segregation of tasks has important consequences for the organization of the colony. Indeed, it has been shown that interactions are much more frequent between ants performing similar tasks [165], and that interaction rates are important regulatory signals for activating and inhibiting workers to perform particular tasks [169-172]. Because activities are segregated within the nest, workers specializing on a particular set of tasks are therefore more likely to interact with other workers with a similar behavioural profile, increasing their ability to share relevant information about their preferred tasks. Moreover, as workers transition towards other behavioural profiles as they age, they might relocate progressively within the nest towards areas better suited to their new preferences, possibly helped by the rate of interactions with workers of the same or of different behavioural profiles.

It is interesting to note here that the spatial segregation of tasks is not necessarily accompanied by the building of barriers to physically separate them. In ants and honeybees, for instance, the brood is often grouped by type (e.g. workers versus drones) or developmental stage within a single space, without walls separating them [30,173,174]. Similarly, the content of honeybee comb cells is often organized spatially, with brood-containing cells grouped together in the centre of the comb, surrounded by a band of pollen-containing cells, and then a larger peripheral region of honey-containing cells, but again with no physical barrier between these different areas [30,163].

The existence of a spatial segregation of tasks without physical barriers is understood to be the result of simple self-organizing processes of differential aggregation [174–177]. This suggests that different areas within a nest-with or without physical separation-might specialize in a particular type of task, not because of their intrinsic characteristics, but because of social feedback loops between the workers: the more a task is performed at a location, the more likely it will be performed again at that location. For instance, in a recent study, Czaczkes et al. showed that Lasius ants will preferentially drop their faeces at specific locations within their nest (usually a specific corner of a specific chamber) [111], separate from other waste materials that are gathered in piles outside the nest (the 'trash') [111]. This behaviour is most likely driven by social signals contained in the faeces (e.g. pheromones) that stimulate ants to leave their faeces where other ants have done it, leading to the creation of, effectively, toilets. This self-organized spatial segregation of tasks [178-182] is at odds with the way it is achieved in human constructions. Indeed, buildings built by humans are planned ahead and each room is pre-assigned a type of task, and then fitted with all the required features for users to accomplish these tasks.

The basic purpose of any building is to satisfy the physiological and social needs of the organism: on the one side, to provide protection and shelter, as discussed above; on the other, to shape and manage activity. The former transmits to all constructions: human and animal; the latter to social organisms (humans and most typically social insects), which build structures that act as a form of enabling device to organize activity and define social conditions. Scrutinizing built structures enables us to consider space retrospectively as a system of social relations from which rules, or patterns, of inhabitation may be extrapolated. For instance, Bill Hillier and Julienne Hanson analysed the organization of built forms and illustrated how the configuration of space changes when specified from the perspective of each distinct area constituting planned arrangements [103]. Identifying the heterogeneity of built forms, they revealed buildings to be systems of activity defined by the dynamics of social and cultural goings-on. Similarly, analysis of social insect nest structures illustrates intricate spatial arrangements and the social structure of the colony [90,183].

Working out the organization of a building is one of the most important and taxing aspects of architectural design. The task of organizing the numerous criteria of a building programme was identified by Rittel and Weber [184] as 'wicked', because planning problems tend to be combinatorially hard. The typical approach to organizing a building is to flatten the problem, so that the activities to be housed can be planned. This has led some, like Paul Coates, to claim the way architects traditionally organize a building is most unnatural [66]. Inspired by the way natural systems are understood as pattern making and problem-solving, architects are today looking to the replication of phenomena in biology and computer science (such as flocking [185], stigmergy [185-188], branching systems [188], food foraging and nest construction [189], replication [190] and so forth) as an alternative approach to modelling form and structure that evades the traditional top-down centralized decisionmaking process of configuration. This has opened up a whole new way of thinking about configuration in architecture, which is bottom-up and generative, and reminds us of Migge's interstitial notion of space whereby internal and external domains are conflated and flow into one another (see the previous section).

The architect Frederick Kiesler (1890-1965), who was strongly influenced by biology [61,191], promoted a notion of space extending Migge. He considered space to be continuous, or endless-not in sense of the void but in terms of a line for which both ends meet. This notion of space, which is evident in both the organization and materiality of his work [192], was informed by what he saw as a fundamental distinction between how humans construct and what he observed in nature. 'Nature [he says] builds by cell division towards continuity while man can only build by joining together into a unique structure without continuity' [193, p. 67]. His point is that humans construct through brute force (connecting parts together to form a whole: we bolt, glue and force elements together). In non-human constructions parts merge, overlap and conjoin one another as a consequence of self-organizing and emergent processes. The concept of stigmergy describing social insect nest construction is a case in point, which we will come back to in §3c(ii). Kiesler sought to emphasize that how we organize space and devise the arrangement of matter is tied to how we comprehend space and distinguish spatial relations.

(iii) Function building

An organism's fitness is not determined by its personal morphological, physiological and behavioural phenotypes only. It is also influenced by phenomena that result from its activity, but are not a physical part of its being [194]. 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 [195,196]. Besides providing protection (as discussed in §3b(i)) and a means to organize the colony's activity (as discussed in §3b(ii)), 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 [35,81,82,145,149,197-200]. This is a common occurrence in large ant and termite nests, in 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 [144,151,153]), 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 [35,149,200]. A similar mechanism was found to be responsible for nest ventilation in the termite Macrotermes michaelseni [198]. 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 [81,82].

In all the examples above, the structure of the nest itself performs the function, independently from the behaviour of the organisms that built it. In many cases, however, the function of the structure only becomes apparent when in interaction with the behaviour of the organism. For instance, topological and geometrical features of ant and termite networks of foraging trails and nest tunnels have been shown to guide the movement behaviour of the workers [19,23,90,91,201–206], 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 behaviour of the organisms.

Similarly, the structure of human constructions performs 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 emphasize 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 1840s 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 2000 vertical shafts, smoke flues and ventilation channels, some up to 200 m 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 [207].

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 Yeang's design was informed by the path of the sun, so the building's form also acts as a shading device reducing solar gain [208]. The form and shape of buildings can also act as a device to distribute people and control the flow of movement. Crowd disasters are a prevailing issue [65,209,210] that has led to extensive data collection to investigate the dynamics of crowd behaviour [211,212]. Serial incidents at the Hajj, Mecca, have resulted in the reorganization of the Hajj, and specifically a new design for the Jamarat bridge. Different levels serve pilgrims coming from different areas and directions to reduce crowding on the Jamarat plaza.

Control is a fundamental factor of institutional buildings, which is clearly evident in Jeremy Bentham's Panopticon. His design is a system of control allowing observation of prison inmates by a single watchman, without the inmates being able to tell whether or not they are being watched. The building acts as a device to prevent, or reduce, the likelihood of undesirable behaviour [208,213]. On a grander scale, Haussmann's plan for Paris remodelled the city to modernize it and also provide physical control of the population. He replaced many narrow streets, which allowed the revolutionaries to establish barricades, with broad boulevards and avenues. Less obviously, the wider streets function as a form of psychological crowd control—a mob may be less likely to revolt due to the expanse making them feel less powerful [214].

(c) Constructions as a way to shape information

All living systems communicate in some shape or form, be it through chemical emission (e.g. scent and pheromone), visual display (e.g. form, colour and movement), sound production (e.g. vocalization and vibration) or electric currents, to inform others of their own state (e.g. mating status) or of the state of their environment (e.g. incoming danger) [215,216]. As hinted at in the previous section, communication can also be achieved through the building. Indeed, each construction act, by modifying the content or configuration of the environment, has the potential of constraining or guiding future behaviours. In Batesonian epistemology, it is 'a difference which makes a difference', that is an 'elementary unit of information' [217]. If we accept that each feature of a construction potentially holds information-or even is information-then we need to discuss the meaning of this concept in biology and architecture. In particular, in this section, we will attempt to identify possible points of agreement and disagreement between the two fields in order to facilitate communication-no pun intended-and collaboration between researchers across the aisle.

The concept of information is rather proteiform in both the scientific and philosophical literature [218]. Scholars in all disciplines have already proposed an uncountable number of definitions of information. With this manuscript, it is neither our intent to introduce a new one, nor to discuss the relative merits of each existing definition. However, in the following sections, we will often refer explicitly and implicitly to two of the most prominent definitions of information that of Claude Shannon and that of Gregory Bateson—and we think it necessary to briefly describe and contrast them here.

Claude Shannon's idea of information [219] is motivated by the need to measure and mathematically describe information in order to quantify differences between messages (e.g. to detect transmission errors) and degrees of dependence between different signals (e.g. to detect phase synchronization between separate sources of information). Rooted in statistics and probability theory, Shannon's information has been hugely influential in many disciplines in science and engineering, because of the analytical tools it provides for measuring and comparing the information content of random variables independently of their meaning. As Gibson points out, Shannon's information excludes the meaning of a stimulus to focus on the quality of message transmission from source to the receiver [110].

Gregory Bateson's ecological view of information is rooted in the cybernetic idea of communication and organization. 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 [217]. This somewhat paradoxical statement deserves unpacking. While Shannon's concept of information is about the 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 [220]. He describes a referencing system that perceives and thereby distinguishes [221,222], 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.

(i) Cues, signals and biological information

In the behavioural sciences, information generated by an organism is traditionally separated into two categories: cues and signals [215,216,223]. 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 behavioural 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 behavioural 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 behaviour of social insects. For instance, the construction behaviours 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.* [224]). 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) [14,29,225] and the final result of the building activity (e.g. walls aligned along the direction of air currents in ants and termites) [224]. Signals, on the other hand, are more often associated with coordinating the actions of the individuals in the colony. For instance, the addition of pheromones to the construction material in ants and termites has arguably evolved to encourage individuals to add to structures built by nest-mates rather than to random environmental heterogeneities [14]. It could also represent the freshness of the material, therefore indicating structures under construction requiring additional actions by workers.

Similarly, environmental and contextual cues are fundamental factors influencing the building and formation of human constructions. Vernacular architecture perhaps best illustrates how determinants such as climate, availability of local construction materials and the influence of local traditions have informed the design of human constructions. One of the most significant determinants is the climate (see §3b(i)). Buildings in cold climates typically have few openings, windows are small or non-existent to prevent heat loss, and have high thermal mass or significant amounts of insulation. Conversely, buildings in warm climates tend to be constructed of light materials to allow cross-ventilation through openings in the fabric of the building. The different aspects of human behaviour and the environment have led to different building forms, evident in the variable contexts and cultures around the world [157,158,226]. Despite these variations, all buildings are subject to the same laws of physics and hence demonstrate significant similarities, which are evident also in social insect constructions: see §3a(i).

However, human constructions differ from that of insects in that they are also the product of socio-cultural factors that escape largely natural selection. As technology has advanced and human socio-culture has progressed with it, methods of construction have become more sophisticated and the form of buildings has evolved. Innovation and technological advancement allow architects to overcome constraints, such as those determining vernacular architecture. For example, the Gothic flying buttress was an innovation transferring gravitational forces to ground in a way that allowed walls to become lighter, which permitted greater expanses of glass and thereby daylight to flood an interior of buildings. Applied to churches and cathedrals this technique of building provided a means to denote divinity and promote the authority of the church. So, human construction is not only informed by environmental/contextual informationlike in social insects-but also enables cultural signs to be embedded in the construction itself. These signs develop through a process typically referred to as 'cultural evolution' [227-231], whereby knowledge, beliefs, languages, etc., are passed on from generation to generation (inheritance), modified over time, and may enter in competition with each other, leading to selection pressures not unlike that underlying natural selection.

(ii) Stigmergy and spatial embedding of information

The notion discussed above that construction—whether by humans or insects—embeds information (or in other words, that it can influence future actions of the builders or the users) is reminiscent of the concept of stigmergy in biology. This idea was first introduced by Pierre-Paul Grassé in 1959 to describe the construction behaviour of termites [186,232]. Grassé explains that the organization of the building activity does not depend on direct coordination between the workers, but rather on indirect coordination achieved through the modification of the structure under construction. Each time a termite worker adds or removes material from the structure, it changes the configuration of the local environment around it. This change will influence subsequent building activities at or around its location, either by the same worker or other workers in the colony. Coordination at the colony level emerges from the repetition of such stigmergic processes, giving the impression that the colony is following some sort of well-defined plan.

As Grassé's original insight, stigmergic coordination has been found to play a role in most constructions built by social insects. For instance, the primitively eusocial wasp Polistes builds its nest out of paper it produces by mixing its saliva with plant fibres [26]. This paper is then turned into walls that will ultimately form a comb of hexagonal cells. During the building of the comb, cells are not added randomly to the structure under construction: wasps are more likely to add new cells where existing cells already form three or more adjacent walls [13,233]. As a consequence of this preference, multiple wasps can coordinate their building activity and will first complete existing rows of cells in the comb before starting a new one. The result of this indirect coordination is a round-shaped comb with approximately 150 cells and, more importantly, without holes. Other examples of social insect construction relying on stigmergic coordination include internal and external structures of nests in ants and honeybees [14,163], trail networks in ants and termites [234-236] and cemeteries and refuse piles in ants [113,224].

While it can be argued that stigmergy is a dominant organizational force in social insects' construction, they also rely on other modes of coordination during building. In particular, environmental and social templates play an important role-often in combination with stigmergy-in determining the final shape of the construction [13,51]. For instance, Macrotermes termites adjust the size of their queen's chamber to match her size as she grows [237,238]. Similarly, rock ants (Temnothorax albipennis) adjust the size of their nest to the quantity of their brood [239-241]. In both cases, it is believed that volatile pheromones produced by the queen and the brood establish a chemical gradient around them that can be used as a template by the workers to determine the size of the construction. Environmental heterogeneities and gradients can also be used as templates by social insects, determining for instance the location at which a construction is initiated or its final orientation. Finally, social insects can use direct coordination to organize their building activity. This is the case, for instance, for the self-assemblages built by some species of ants (e.g. temporary nests, bridges and ladders) and bees (e.g. swarms and festoons) by attaching to each other [12,37,38,47,49]. While limited to a few species, these-quite literally-living architectures built through direct coordination have the advantage over stigmergic structures of being extremely plastic and reactive, sometimes assembling and disassembling in a matter of minutes or even seconds.

As a concept to describe the coordinated building activity of social insects, the concept of stigmergy does not, on the first inspection, easily transfer to human society and its architecture. However, Grassé's idea of stigmergy can be extended to encompass all forms of cues and signals that organisms including humans—leave in their environment that have the potential of mediating indirect interactions between individuals [51,186,187]. Stigmergic traces represent the information that organisms embed in the spatial context and, together with environmental influences, they define a large part of the information landscape accessible to each organism.

In the social sciences, Grasse's original insight has been studied in the context of numerous forms of human activity, including the stock market, economics, traffic patterns, urban development and more besides [242-245]. One may claim even that the way architects design traditionally, through drawing sketches, is stigmergic, whereby a line drawn on the page breaks the homogeneity of the blank surface, and influences scribing the next line. Successive lines are added influenced by and influencing the developing pattern to mediate the development of an idea. Working in a team, the same sketch is referred to and developed by others who are influenced by what they see and add to, adapt or emphasize aspects of the sketch. Building Information Modelling uses a stored digital model, which is accessible to all members of a design team, who work on and develop the model in parallel, detecting clashes and developing the model collectively. For an explanation see the National Building Specification (NBS) at https://www.thenbs.com/knowledge/what-is-building-information-modelling-bim. Recently architects have begun investigating stigmergy as a mechanism of coordinating design and construction [245] and experimenting with stigmergy as a method of generating form [246-248,249] and organising activities [250, 251].

As mentioned earlier (see §3b(ii)), the capacity to use the computer to simulate the autonomy, emergence and distributed functioning of natural systems provides architects with a new way of producing form and structure, and to think about the organization of areas constituting a building or city. Adjacency and circulation are fundamental concerns in organizing architectural layouts, because of factors like the movement of people, material and information between areas, and/or the need to control or supervise one area from another. The nature of such problems has been characterized as 'wicked' [184] because of the interrelatedness of the factors involved. The food foraging behaviour of ants, for example, has been explored as an alternative method of organizing distribution networks in buildings and cities. Instead of placing activity areas in relation to one another based on convention, the stigmergic behaviour of assorted artificial ant colonies has been used as a method of self-aggregation, and applied to generating the desired arrangements between activities in a building [252], and to generate primitive room arrangements [250]. Puusepp proposed a model whereby circulation is developed as an emergent by-product of global morphogenesis of the built form [253], and proposed a tool for generating outline urban arrangements often associated with unplanned settlements [254]. The stigmergic behaviour evident in insect societies and animals has also been adopted as a method of form finding [247,249,255]. Carranza and Coates, for example, used the trails left behind by a population of swarming agents as a scaffold to wrap a continuous surface around [247].

While stigmergy has been applied as an alternative approach to organizing buildings and form finding, the casual form of urban aggregation evident in medieval villages, Brazillian favelas and Chinese Hutongs exemplifies stigmergic configuration driven by environmental constraints, as with vernacular architecture, but urban aggregation of this type is also driven by associations with one's neighbour. While cities are prone to top-down planning by the authorities, they have been shown to operate as a dynamic, adaptive system based on interactions with neighbours, feedback and decentralized distribution of people, goods, information and energy [70,256,257]. Consequently, urban growth has been evaluated computationally and illustrated to replicate natural systems [66,258]. Coates demonstrated how the formation of early human settlements is underpinned by geometrical constraints that inform the arrangement of unplanned as well as planned urban arrangements through a combination of environmental feedback and simple local rules [259]. The algorithmic approach driving contemporary architectural design today is motivated by this comprehension of geometrical rules and stigmergic behaviour of agent-systems evident in shaping urban settlements and the configuration of buildings. Coupled with the capacity of social insect societies to unscramble the wickedness of certain problems (like searching for food), architects are today looking to the decentralized and distributed control evident in the behaviour of social insects and how they form the structures they build [13,51,189].

(iii) Explicit and implicit information

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

Implicit information, on the other hand, corresponds to features that can modify the behaviour of an organism without requiring this organism to process or even perceive the associated stimuli. In other words, they are features of the physical and social environment that do not have a meaning for the organism-the organism might not even be able to perceive them-yet they may influence its actions in a manner that the organism cannot control. These are often external physical forces applied on the organism without its knowledge (e.g. the tide pushing planktonic organisms toward the shore) [260] or barriers that constrain the movement of the organism. In some species of ants, for instance, it was found that the geometry of their networks of foraging trails is asymmetrical: when a forager comes back towards its nest and reaches a branching point, the trail heading towards the nest after the branching point deviates less (approx. 30°) from the ant's original direction than the other trail (approx. 120°) that leads away from the nest [17,203,204,206,261]. While one species of ant may be able to use this information explicitly to navigate its trail network [204], others do not seem to perceive the difference and simply follow the path

of 'least resistance' [91,203]. As a result, they are more likely to find their way back to the nest and their foraging output will be increased up to three times, all of this without requiring any navigational capabilities, spatial awareness or even the ability to detect the configuration of the branching point (as demonstrated using robots) [205].

Most studies on the building behaviour and construction use of social insects involve characterizing explicit forms of information: pheromone deposits, tactile contacts, air movements, etc. [14,224,262]. Few, however, have considered the importance of implicit information in shaping the collective behaviour of the colony. Indeed, one difficulty with studying implicit information is that it is not always obvious to an external observer given the disconnection between this form of information and the sensory and cognitive apparatus of the organism. Yet, as in the example mentioned above, there is strong evidence that the topology and geometrical organization of the environment have an influence on the spatial distribution of organisms, even when they are imperceptible to said organisms. Therefore, it should be explored more systematically in the context of social insect constructions.

Similarly, we can see examples of information that is embedded within the human-built environment, and in architectural form, and how it too can have an influence on the behaviour of the perceiver. Again, this impact may be described as implicit or explicit. Winston Churchill's adage 'we shape our buildings; thereafter they shape us' exemplifies the built environment as a chief factor in determining behaviour. The correlation between perception of the environment and its implicit effects on well-being and behaviour has long interested psychologists [263]. The complexity of the built environment is a crucial factor contributing to human behaviour. Experiments measuring how the brain and body respond to different kinds of settings show people are bored and unhappy when faced with extensive bland facades, and by contrast, happy and stimulated by varied and permeable building frontages, which will in turn have an influence on where a person will choose to spend their time [264,265].

Quantitative theories and methods of analysing urban configurations, such as Space Syntax [266], illustrate the correlation between the geometrical composition of the built environment and social behaviour [103,104]. Graph-based representations and statistical analysis of the structural properties of built form illustrate that there is a direct correlation between the topology and geometrical organization of the environment and the spatial distribution of people and movement [267-269]. For example, the least angular deviation along a route suggests the structure of the street network is itself the key determinant of pedestrian flow. A pedestrian will tend to choose routes that require the least amount of turns, and this will correlate to their perception of how well integrated the street is within a network, and consequently to pedestrian density. The implication is that configuration can have effects on movement that are independent of attractors [270,271].

The role of explicit information in the built environment is both more literal and more formalized. Road signs and the demarcation of pathways are obvious examples. In extreme cases, the function of the building is literally interpreted by the observer, such as 'Big Duck': a shop selling ducks and duck eggs that is built in the shape of a duck. However, a particular aspect that distinguishes the human use of information is our capacity to build arbitrary associations between things and to think metaphorically. Symbolism enables humans to communicate with other humans they do not meet: i.e. symbols are an indirect form of communication, which are embedded and perceived throughout the built environment and have developed their associations (or meanings) through cultural evolution. A structure is symbolic when it acts as a vehicle of arbitrary content and the observer reads the embedded meaning, making architecture 'other than' just a building, as discussed in §3a(iii).

4. Conclusion

Humans have long since looked on the natural world as a source of inspiration, and observation of what other animals can do has driven us to achieve feats beyond our natural capabilities; such as being able to fly. The idea of late that simple creatures build complex and dynamic constructions has spurred researchers to investigate the mechanisms behind such phenomena, from the building of social insects' nests to the formation of cells, tissues, organs and ultimately organisms. The complex and coordinated behaviours resulting from interactions between individuals in a collective has led scientists and engineers to question how this understanding may be applied to human-related problems. Architects, on the other hand, who are becoming more aware of the parallels between biological processes and design, as well as the artefact-making capacities of animals, are turning more to biology to explore innovative methods of problem-solving and designing.

While there is a long history of biology influencing architectural endeavour, only recently have biologists and architects begun to meet and collaborate. As indicated at the start of this paper, this union brings inherent difficulties as each discipline claims its own high ground and concepts fundamental to both are viewed distinctly from either side-perhaps none more so than the concepts of 'architecture', 'space' and 'information', which are not only fundamental to the sciences and humanities but to everyday understanding. Consequently, we set out in this review to cross-examine these concepts in biology and architecture and to establish a framework within which fundamentals that span both disciplines are apparent and beneficial to both, with the view to better enabling cooperation in the study of constructions built by social organisms and how these structures influence, direct and manage behaviour of social systems.

The primitive framework established here provides a basis on which to build. Having examined the notion of

architecture, we have proposed an open definition spanning human and non-human constructs and reviewed the concepts of 'space' and 'information' in relation to human and social insect constructions. Additional concepts, such as 'emotion', may be scrutinized and included to facilitate and bolster interdisciplinary discourse. The notion of delight is perhaps beyond scientific reason, but aesthetics (if we refer to Baumgarten [121,122]) may be considered a fundamental aspect of all living systems. The key, we suggest, is to analyse the occurrence of internal-external relations established by perceptual systems in the process of distinguishing information about their world. The real issue is to avoid anthropomorphizing the social insect and consider how the insect's perceptual system conveys information about its world. In so doing, we should avoid seeking the meaning and establish the internal-external relations that inform, direct and lead to, for example, the termites' pillar building activity. Living systems are embedded in their environment, which, we have proposed, from the organism's perspective, is a matter of relations and forms that influence behaviour. These features, which may be evolved (signals) or not (cues), perceptible (explicit) or otherwise (implicit), constitute environmental pressures that constrain and coerce the activity of organisms. Spatial constraints are a fundamental feature of living systems, both in their development and in their unfolding engagement with the world [272,273]. Evident, for example, in the building of self-ventilating mounds in termites, the rules that govern construction can be seen as productive constraints because they are sensed by the organism that responds to it, giving it a meaning, and ultimately creating a functional pattern (the mound and its passive ventilation) that improves the colony's fitness. It is a fundamental character of natural systems that spans scales from abiotic to social systems. This semiotic perspective unifies architecture and biology and, we hope, could be the basis for a more formal collaborative language between the two disciplines.

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Review



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The impact of the built environment on health behaviours and disease transmission in social systems

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The environment plays an important role in disease dynamics and in determining the health of individuals. Specifically, the built environment has a large impact on the prevention and containment of both chronic and infectious disease in humans and in non-human animals. The effects of the built environment on health can be direct, for example, by influencing environmental quality, or indirect by influencing behaviours that impact disease transmission and health. Furthermore, these impacts can happen at many scales, from the individual to the society, and from the design of the plates we eat from to the design of cities. In this paper, we review the ways that the built environment affects both the prevention and the containment of chronic and infectious disease. We bring examples from both human and animal societies and attempt to identify parallels and gaps between the study of humans and animals that can be capitalized on to advance the scope and perspective of research in each respective field. By consolidating this literature, we hope to highlight the importance of built structures in determining the complex dynamics of disease and in impacting the health behaviours of both humans and animals.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

The health of individuals and populations is affected by the environment in which they live. Some environments harbour more pathogens than others and population densities vary across environment, which influences disease transmission dynamics. Moreover, variation in resource distribution across environments can determine movement patterns, which can expose individuals to new pathogens, but also contribute to their health by increasing activity. The built environment can be modified to promote healthy behaviours and reduce the risk of contracting a disease.

Perhaps the most striking illustration of how the built environment can affect both health behaviour and disease comes from the history of urban planning over the past century [1–4]. Disease was the raison d'être for the advent of urban planning in Europe and the USA, and one of the central motifs that shaped architecture of modernism. Throughout the nineteenth and early twentieth century, urban environments such as London, Paris, New York City and Chicago were densely populated and characterized by residences in proximity to factories, animal yards, slaughter houses and crowded tenement houses with little airflow or light. The cities were plagued with epidemics of infectious disease. Waves of cholera, tuberculosis and typhoid swept through these cities, wiping out significant portions of the population. Disease was not well understood at the time and models such as 'miasma theory'—that 'bad air' vapours transmitted pathogens—prevailed. However, there was a sense that the congestion, pollution, lack of sunshine and poor airflow contributed to illness. In response, the mid-nineteenth century public health movements [5] and the extensive rebuilding of European and North American cities ensued, with the aim of improving the overcrowded and unsanitary urban living conditions [6,7]. Zoning, i.e. separation of uses, was introduced to spatially segregate residential, commercial and industrial uses, and housing regulations required light and air flow. Remarkably, these efforts to configure the built environment to control infectious disease in the late 1800s and early 1900s ultimately contributed to chronic diseases in the twenty-first century.

The separation of uses through zoning and development of suburbs, along with the advent of the automobile, led, 100 years later, to environments that discourage walking and promote movement in the private automobile. We now have a physically inactive population with rising rates of obesity and related chronic diseases such as diabetes, cancer and coronary heart disease. The field of urban planning and, to some extent, architecture have now-since the early 2000srenewed partnership with public health to respond to the new health crises: physical inactivity, poor diet and obesity. In an attempt to curb the obesity epidemic, urban planning efforts have begun to target both sides of the energy balance equation—diet and physical activity [8]—by considering the accessibility, availability and affordability of healthy foods and aspects of the built environment (e.g. density, mixed use and design features) to encourage physical activity. In addition, there is growing recognition that low-income and minority neighbourhoods are often 'food deserts' characterized by the abundance of liquor stores and fast food restaurants but with a dearth of grocery stores. On a parallel front, the relationship between mental health and the built environment, in particular in urban centres, is becoming an equally important concern. Chronic disease, such as depression, has been linked to both social and physical aspects of the built environment-from factors such as social isolation and poverty in the neighbourhood to housing quality, crowding and urban design of streets and green spaces [9-11]. Current designers' proposals for addressing these mental health issues include the creation of spaces supporting physical activity, social interaction and high-quality access to nature, and are thus coinciding with the design strategies for improving the physical health of the population.

The history of urban planning in the past century highlights the effects that the built environment can have on both the prevention and containment of chronic and infectious diseases. Chronic disease is defined as a noncommunicable disease that persists for a long time and that cannot be prevented by vaccination or cured by medication. Infectious disease is caused by pathogenic microorganisms and can spread among individuals. Strategies for battling both types of disease includes pre-emptive preventions, such as hand washing and vaccinations for infectious diseases, and health-promoting behaviours, such as an active lifestyle and healthy food habits for chronic diseases. Once a disease becomes prevalent in a population, containment becomes the main strategy for defence. For example, quarantine of diseased individuals in the case of infections and caring for sick individuals and improving their environment in the case of chronic disease. Non-human animals are also prone to both chronic and infectious diseases and they too engage in prevention and containment behaviours. Ways that the built environment can facilitate the prevention and containment of disease in non-human animals include the type of building materials that are used and the way built structures organize the society and promote or prevent certain interactions. Thus, the built environment can promote both the containment and prevention of chronic and infectious disease in human and non-human animals.

The built environment can affect health directly and indirectly either through immediate, passive impact (e.g. effects of indoor environmental quality) or by influencing behaviours that can affect health, which can involve individuals' active participation (e.g. encouraging walking to increase physical activity). It is worth noting that the definitions of human health and disease are products of history, politics, economics and culture [2]. In this sense, the notion of what it means to be healthy or sick is guided not only by the available medical knowledge, but also by broader social and cultural factors. For most of the nineteenth and twentieth centuries, medicine was concentrated on pathology and finding ways of treating/curing disease. However, as societies experienced an epidemiological transition [12]diminishing infectious disease and increasing the prevalence of chronic diseases-the idea of health-related quality of life has emerged as an instrument to cope with the new situation [13]. Accordingly, the current understanding of health is not only as an absence of disease but also as a state of complete physical, mental and social well-being, which holds prevention as important as cure and looks for long-term solutions [14,15]. This idea is reflected in the current design approaches to health problems and what is considered as a problem; the aim of architectural and urban designs and behaviour interventions is to enhance overall well-being through mental and physical health.

Prevention and containment of disease can happen at many social and biological scales, given the multilayered physical, social and socio-economic context of the built environment. For example, at the society level, governments can establish policy, which impacts states, counties, schools and individuals. Individuals, in turn, may take actions to impact their immediate environment, regardless of global policy. Modelling approaches in biology scale from agentbased [16], to population, to evolutionary models, and each level provides different insights on disease dynamics. The scale at which actions take place can impact what proportion of the population is affected and how quickly remediation can occur. Considering scales of action is important when discussing the design of the physical environment. In this sense, three scales are of particular relevance: the urban, architectural (or building) and behavioural design. Urban design and planning can impact population-level processes by affecting the proximity of individuals to one another, while at the architectural scale, with the help of behaviour and product design, spatial structures and targeted interventions can impact individuals' behaviour, thus promoting local changes.

In this paper, we review the impact of the built environment on both chronic and infectious disease. For each, we detail ways that the built environment has been and can be used for prevention or containment through examples from both human and animal societies. Through this review of the literature, we attempt to identify gaps between the study of humans and animals that can be capitalized on to advance the scope and perspective of research in each respective field. For example, the scale at which containment action is taken in human societies might inform the conservation of animal populations, and the evolutionary perspective that often characterizes studies of animal behaviours might inform prevention strategies for human disease. Our goal with this review of the literature is to set the groundwork for further, more in-depth studies of each of the various ways that the built environment affects health behaviours and disease dynamics in humans and non-human animals.

2. Chronic disease

(a) Prevention in humans

In this section, we consider how the architecture of the human environment can contribute to the prevention of chronic disease-related to both physical health and mental health. We consider three themes to illustrate health-promoting qualities of physical environment. First, we consider how the physical environment (at the urban, architectural and behavioural scales) promotes physical activity, which helps to prevent obesity and the associated chronic diseases including diabetes, heart disease and cancer. Second, we describe how the built environment affects dietary habits, another important factor in obesity. Third, we consider the effects of housing and urban design on mental health. These three themes are representative of the main research topics in current health-related design, and the possibilities available for promoting health and preventing chronic disease through the built environment.

(i) Physical activity

In recent decades, recognition that the built environment can affect physical activity or inactivity has led to efforts that leverage the environment to promote physical activity and thereby reduce the prevalence of associated chronic disease. This realization has resulted in a reconnection of urban planning and public health, two fields that united in the early 1900s to combat infectious disease and then had little association for many decades. Planners summarize the features of the environment influencing physical activity at the urban or neighbourhood scale by referring to the '3 Ds': density, diversity and design [4,17,18]. Density refers to the compactness of physical infrastructure (i.e. distances between buildings and functions). With more proximate destinations, residents are more likely to walk rather than drive a vehicle. Diversity refers to 'mixed use'-in other words, combining residential and retail within the community. This notion is a reversal of the segregation of uses that occurred in the early twentieth century in response to infectious diseases. Diversity means that there will be walkable destinations near the places where people live. The third D, Design, is relevant on various levels. Neighbourhood design has been revisited via neotraditional or new urbanist neighbourhoods that are pedestrian-, rather than car-focused. Such pedestrianoriented designs have small lots, short setback distances (i.e. distance from the street to the front of the building), porches and sidewalks, in contrast to car-oriented suburbs that typically have 1 acre (or larger) lots, large setbacks and no sidewalks. The features of neotraditional communities promote social interaction, sense of community and walking [19]. People who live in neighbourhoods with a grid-like street network pattern also tend to drive less than those

living in other kinds (e.g. suburban 'loops and lollipops') of street networks [17]. Design further includes smaller-scale design elements, such as street lights and benches, that make a place pleasant and comfortable for walking. In recent years, a fourth and fifth D have been added: Destination accessibility (i.e. ease of travel to a central business district) and Distance to transit (i.e. the average distance from the residence to the workplace or to the nearest train station or bus stop) [18].

Building design can also be employed for its potential to encourage physical activity. For example, placing a stairway in a salient location and making it inviting and aesthetically pleasing, while locating elevators in a less obvious, less central position, may encourage stair use [20]. Colour, music and artwork have been used to encourage the use of stairs [21]. These efforts to design buildings to promote physical activity are ironic in light of research a century ago aimed at essentially the opposite goal: 'saving steps' by improving the efficiency of daily tasks [22]. In 2010, New York City published 'Active Design Guidelines' encouraging design decisions to help promote physical activity [18]. The guidelines address building design and urban design strategies. On the building scale, four key themes are identified as most critical to promoting physical activity [18]:

- Building circulation system. The design of the 'connecting spaces' such as corridors, stairways, elevators and lobbies can play a critical role in encouraging physical activity within a building.
- Building elements. The availability, safety and comfort of spaces such as stairs, shower rooms and bicycle storage as well as smaller details such as the presence and location of drinking fountains and benches can promote movement.
- Organization of the building programme. Configuration of the activities within the building can help to ensure that physical activity is 'built in' to daily activities. For example, daily tasks that require physical activity include going to a central location to retrieve mail, get coffee, or pick up lunch. These strategies employing intentional distance or inefficiencies are referred to as 'functional inconvenience' [23].
- Activity spaces. Building areas specifically programmed for physical activity can also contribute to occupants' total physical activity. These spaces include swimming pools, running tracks and exercise rooms.

Research has also begun to examine the effect of smallscale environmental changes on increasing physical activity or reducing sedentary behaviour, particularly within the workplace. Neuhaus et al. [24] reviewed the evidence regarding the influence of 'activity-permissive' workstations, including fixed standing desks, height-adjustable desks, treadmill desks, cycle ergometers and pedal devices fitted under the desk. Of the 14 studies that examined effects on sedentary behaviour, 11 found a significant effect of the intervention with an average reduction in workplace sedentary time of 90 min per 8-h workday. Other researchers have begun to study the influence of architectural design in combination with activity-promoting furniture within the school environment [25]. Dutch architects RAAAF (Rietveld Architecture-Art Affordances) have responded to society's epidemic of sedentary behaviour with the 'End of Sitting', an art-architecture-philosophy installation that questions

the inclusion of desks and chairs as default components of the workplace and imagines what a space that affords supported standing and varied postures might look like [26].

Finally, the field of behavioural economics [27], a cousin to environmental psychology, offers additional insights regarding the possible influence of context on physical activity. For example, social norms can be used as 'anchors' to influence behaviour. By intervening in people's perceptions regarding what are 'normative' or typical levels of physical activity, people might become more active. Framing physical activity as fun, rather than obligatory, could also affect people's likelihood to engage in physical activity [28]. Related to these themes, both policies and physical infrastructure can, together, affect physical activity norms. For example, making public transportation affordable, providing biking lanes and making automobile parking expensive can encourage walking and biking, and discourage driving.

(ii) Diet

In parallel with studies examining the association of neighbourhood design characteristics with physical activity, other studies have been examining the association of neighbourhood features with dietary intake or obesity. A study of the New York City food environment found that access to healthy food stores was inversely associated with body mass index and obesity prevalence [29]. Another study of more than 3000 New Orleans residents found that after adjusting for individual characteristics, each additional supermarket in a respondent's neighbourhood was linked to a reduced likelihood of obesity, while fast food restaurants and convenience stores were associated with greater obesity odds [30]. Research also indicates that disparities in access correspond to disparities in dietary intake. For example, in a study of African American boys, greater availability of vegetables and juice at local restaurants was associated with greater juice and vegetable consumption [31]. In a rare natural experiment, Wrigley et al. [32] found that when a new grocery store was constructed within a 'retail-poor' area, consumption of fruits and vegetables (FV) increased significantly among those with the most FV-deficient diets.

On the building scale, research has begun to examine how design features affect dietary intake. In the grocery store, Cheadle et al. [33] found that the proportion of shelf space dedicated to healthy foods, such as low-fat milk and dark bread, was associated with individual dietary practices. The effects may be similar within the home environment. Open layouts, which provide visual access between the kitchen and the living room, may encourage trips to the kitchen and increase food intake [34]. In addition, research indicates that smaller-scale environmental and product design features also affect dietary intake. Larger plates, portions and packages influence people to consume more [35-37]. In addition, people tend to eat in 'units'; in other words, typically, a person eats the entire item, regardless of the size of the muffin or cookie [38]. Fortunately, small-scale environmental features such as plate size can be modified to mitigate over-consumption [39].

(iii) Mental health

In addition to its effects on health-related behaviours and physical health, the built environment can affect mental health, both positively and negatively. In the light of current urbanization rates and evidence suggesting that city dwellers have higher risks of mental health problems, such as depression and anxiety, compared to inhabitants of rural areas [10,40], the relationship between the urban mental health and design has recently gained importance. The physical and social environments of urban life can influence the mind and the body at the neurophysiological and psychological levels, and thus affect mental well-being [41,42].

Environmental properties such as spatial layout, architectural features, traffic intensity, noise and pollution can have a direct impact on physiological and psychological stress mechanisms. For example, at the urban scale, the spatial configuration of the city and, more specifically, environmental properties such as typology of open public spaces (e.g. park, square and street), building density and local integration of street segments (i.e. how well a street segment is integrated in the wider city network and traffic patterns) can be used as predictors of urban stress [43]. Researchers found that high values of local street integration, which is associated with good walkability, are associated with low stress, while large streetscapes and squares with low detailing and complexity in building facades are more likely to be perceived as stressful.

Although only depression is currently considered a chronic mental disease, stress and anxiety cannot be excluded as factors affecting the well-being of people in cities because prolonged and cumulative exposure to cortisol can lead to physical chronic diseases like stress-induced hypertension [9,44]. Indirect effects of urban environments have been associated with psycho-social processes, such as personal control, crowding and presence of social networks and support [41,45,46]. Thus, physiological and psychological stressors have the capacity to influence mental health both at the individual level (e.g. individuals' perceptions of the environment) and through neighbourhood effects (e.g. the experience of neighbourhood walkability and state of maintenance and upkeep).

Because both the physical and social aspects of the urban environment impact mental health and well-being, design strategies aimed at preventing or diminishing the negative effects and emphasizing the beneficial ones typically rely on the interplay between these two dimensions. Specifically, a recent report on the 'Five Ways to Well-being' [47] illustrates how the social-physical interdependency can be used in the design of architectural and urban spaces [14,48]. Three of the five points are relevant here. First, the 'connect' idea correlates the quantity and quality of social connections with reported well-being and physical health. In the built environment, this is translated in the emphasis on designing everyday public spaces, especially at the neighbourhood scale, to create opportunities for people to see, hear and connect with others [49-51]. However, social interactions are also tightly connected with density and crowding, which have been linked with increased stress and anxiety [52,53]. Second, the 'keep active' point emphasizes the link between physical activity and well-being, which, in addition to effects on physical health, as detailed above, is associated with beneficial effects on mental health problems, like depression, and thus requires designing more walkable and pedestrianfriendly neighbourhoods [54,55]. Third, 'take notice' considers the benefits of mindfulness and paying attention to the present as a way to reduce the symptoms of stress, anxiety and depression. In the urban environment, 'taking

notice' can be achieved through art, landscaping, wildlife features and seating [14,56]. Overall, the availability of diverse open public spaces, the high density of mixed-use development that encourages walking and cycling, and access to high-quality green spaces in the city can be linked to the positive effects of the physical and social urban environment on mental health. While some of these aspects have been better investigated, many mechanisms, e.g. how the physical environment impacts the mind–body at the neurophysiological level and how this, in turn, might modify behaviours, are still unknown.

Housing quality, housing type and floor level are three aspects of housing that have been associated with mental health outcomes [57]. The relation between housing quality and mental health may be mediated by social withdrawal. In other words, poor housing quality can lead to increased social withdrawal which, in turn, leads to poor mental health [58]. One aspect of housing is interior density, i.e. the number of people per room. Density, a physical, objectively measureable phenomenon, affects crowding, a psychological phenomenon, which in turn negatively affects psychological well-being or mental health. The linkage between crowding and mental health is explained by a disruption of socially supportive relationships among residents of a crowded home. To cope with chronically crowded conditions that provide limited ability to regulate social interaction, occupants often socially withdraw. However, by allowing opportunities to control social interaction, architectural interior design can help to reduce the need to socially withdraw and thereby dampen the effect of crowding on mental health. Evans et al. [59] found that homes with greater architectural depth-the number of spaces one must pass through to reach rooms of the home [60]—buffer the impact of density of mental health by reducing social withdrawal. Complete social isolation can also impact mental health negatively [61–63], and so, the built environment should balance the ability to avoid crowding without risking the isolation of its occupants.

It is important to note that these effects of architecture on the prevention of chronic disease in humans occur within a larger, complex ecological system [64] and thus are not simple, direct effects. Rather, a variety of moderators or 'effect modifiers' influence the valence and strength of the impact of the environment on human health and healthrelated behaviours. This notion is illustrated by Evans et al.'s findings [59] that architectural depth moderates the effect of crowding on mental health. Similarly, Fich et al. [65] showed that when exposed to a strong social stressor (simulated job interview), the features of the built environment-presence or absence of openings in the roominfluence how fast participants recover from stress (measured as cortisol levels). Thus, architecture might modulate people's physiological response in the case of acute stress events, including social situations. Further research is necessary to understand the role of built spaces in the case of acute as well as prolonged or chronic stress, especially when their causes are found in a complex socio-economic network.

Overall, it should be emphasized that the scale of effects resulting from interactions between social and physical environmental factors is still an open question. The aim of this paper is to highlight the myriad ways that the built environment shapes social relations and behaviour in space, and in turn affects human health.

(b) Prevention in animals

Chronic diseases in animals are most commonly found in domesticated and zoo animals. However, some chronic conditions, such as long-term stress and nutritional deficiencies, can impact wild animal populations. Specifically, chronic stress can decrease animals' survival in the wild [66] and increase their susceptibility to infectious diseases [67]. In this section, we detail how stress, diet and physical activity may be impacted by the built environment in animals.

(i) Stress

Built structures can prevent chronic stressful conditions if they provide an enriched physical and social environment. Many industries have been impacted by the interaction between the built environment and chronic stress, including zoos, biomedical research and agriculture. Zoos have been increasingly considering enclosure designs that provide animals with enriched environments to reduce stereotypical behaviours, such as pacing and other repetitive movements, which can lead to chronic heightened physiological stress, i.e. high cortisol levels [68,69]. Built structures that facilitate social interaction reduce stress because grooming in primates and ungulates alleviates stress through the release of β-endorphins [70-72]. Housing conditions of research animals may impact their physiology, thus biasing the results of scientific studies. For example, housing conditions of rhesus macaques can influence their social environment, elevating their stress levels if they are housed alone, which can bias the results of biomedical research [73]. Housing conditions that lead to stereotypical behaviour of rodents used for research may affect the validity, replicability and reliability of studies through changes to animals' brain function [74]. In agricultural settings, the structure of rearing enclosures can influence long-term chronic social stress. For example, piglets raised in an enriched environment do not develop social stress later in life, but piglets reared in a featureless environment (simple farrowing crates) develop chronic social stress [75]. Finally, the chronic stress of wild animal populations can be impacted by built structures. For example, great tits in urban environments express more genes related to stress responses than rural birds [76]. Thus, the built structures that humans construct to hold animals, whether in zoos, laboratories, farms or cities, can have a great impact on the chronic physiological conditions of the animals, which affect their fitness, welfare, utility for scientific research and economic output.

(ii) Diet

Structures built by the animals themselves (rather than by humans) that allow for food storage or acquisition can buffer nutritional deficiencies that compromise animals' health. For example, social insect nests often include chambers that are dedicated to the storage of seeds [77]. Honeybees store nectar in the form of honey, and pollen for protein, at specific locations in their hive [78]. These food stores can ensure colony survival during the winter months, when there are no flowers [79]. Spider webs and beaver dams are structures that assist animals in collecting food [80], thus potentially reducing long-term nutritional deficiencies. Finally, bird nests and carnivores' dens provide both protection from predators and reduce the amount of energy spent by parents caring for offspring by restricting their movements in search of food [81] and by reducing the energetic costs associated with carrying offspring [82].

(iii) Physical activity

In contrast with humans, physical activity might not necessarily promote long or healthy lives in non-human animals. For example, in social insects, queens that are long-lived (more than 30 years in some species) are extremely sedentary, compared to workers who are very mobile, yet short-lived (mostly up to 1 year) [83]. These differences between queens and workers likely stem from differences in metabolic rates [84], genetics [85,86] and exposure to dangers. The high activity of workers leads them outside the safety of their nest, exposing them to dangers such as predation and desiccation. Thus, the built environment, i.e. the ants' nest, provides shelter that may promote longevity. In mammals too, captivity can increase longevity, especially for species with a fast pace of life, for whom captive conditions, such as zoos, provide protection from predators, intraspecific competition and disease [87].

(c) Containment in humans

Despite the efforts to prevent chronic diseases, like obesity and depression, through the built environment, some illnesses-especially those that are age-related-can only be prevented and postponed to a certain point. For this reason, an important part of design interventions in the physical environment is aimed at the management of chronic conditions, i.e. developing and maintaining the systems of care. In this section, the issue of care is considered in three ways. First, we discuss how the social and material environment can serve as the support system in the context of diseases that follow the ageing process, and what kinds of transformations at the urban, neighbourhood and architectural scales can be implemented as strategies for 'caring through design'. Second, we explore the potential of the built environment as a therapeutic tool to alleviate or diminish the effects of everyday stress and anxiety. We further discuss the topics of biophilic design and cognitive restoration as elements of passive design care, i.e. treating lifestyle consequences by directly affecting individuals without requiring active participation or behavioural changes. Finally, we raise the question of care in the context of geographical disparities in health and the issues stemming from the lack of care in the state of the built environment.

(i) Lifetime care through design

The global increase in ageing populations and corresponding age-related physical and mental illnesses such as cardiovascular conditions and dementia, coupled with sensory impairments and reduced mobility, present a public health challenge that can be partially answered through the design of built environment. Over the past decade, different ageand dementia-friendly design strategies for urban and architectural spaces have been developed under the common theme of 'ageing in place' or 'lifetime neighbourhoods'. The guiding principle behind these strategies is supporting active and independent involvement in local communities to maintain health and manage existing long-term conditions in older individuals. For example, at the urban and neighbourhood levels, dementia-friendly designs target the critical issues such as ease of wayfinding by proposing environments that are familiar, legible, distinctive, accessible, comfortable and safe [88]. Some of the key design features include the presence of small, open public spaces with a variety of activities and features, walkable neighbourhoods, architecture with distinctive local character and identity, public seating and ground-level building access as measures of accessibility-in short, all environmental characteristics that encourage physical activity and social interaction as beneficial for physical and mental health in older people. This is in accordance with recent studies indicating the links between social deprivation and depression in high-density cities like Hong Kong [89] and negative effects of deprived and deteriorated neighbourhoods on physical activity [90,91]. These health-related urban design interventions are effective for most age groups. However, it should be acknowledged that some policies, such as active design guidelines, can lead to segregation of various user groups (e.g. young, mobile individuals versus individuals with reduced or no mobility [92]) that call for the development of inclusive approaches.

The possibilities of caring through design for individuals with chronic disease such as cancer have been explored at the architectural scale of healthcare institutions. A well-known example are Maggie's Centres, which were established with the idea that psycho-social interventions increases patients' chances of living longer [92,93]. These buildings are designed to offer cancer patients a place to interact with doctors and families outside of the stressful setting of a traditional hospital and provide a sense of home, through architectural design.

(ii) Therapeutic design and nature

Although we are only starting to understand how architectural and urban environments can act therapeutically on human minds and bodies, designers have been intuitively exploring these capacities for their restorative effects, in particular for the purposes of managing stress and stress-related diseases. Recently, the idea of biophilic design has linked the extensive body of research on the health and stress-relieving benefits of nature and the innate human inclination to seek connections with nature, life and life-like processes; essentially, biophilic design emphasizes the necessity of maintaining, enhancing and restoring the beneficial experience of nature in the built environment [94].

Views of and access to nature have been linked to a wide variety of health outcomes (see reviews, [95,96]). Nature can contribute to the management of stress and stress-related diseases. For example, recent studies by Japanese researchers examine the practice of 'Shinrin-yoku' or 'taking in the forest atmosphere'. In a series of studies, male college students were randomly assigned to walk in the city and then in the forest, or vice versa. Results indicated lower levels of blood pressure, pulse rate and the stress hormone cortisol along with increased parasympathetic nerve activity and lower sympathetic nerve activity following the forest walks compared to the urban walks [97].

For people with disease diagnoses, nature can enhance their capacity to cope effectively. Cimprich [98,99] studied women recently diagnosed with breast cancer and found that patients randomly assigned to a nature intervention showed significant improvements in attentional capacity in the weeks following surgery, compared to those in the non-intervention group. Underlying this work is Attention Restoration Theory [100], which suggests that we have two types of attention: effortful 'directed' attention and 'involuntary' attention that is captured easily and effortlessly. With use, directed attention becomes fatigued, resulting in difficulty focusing, distractibility and irritability. The natural environment engages involuntary attention and allows the mechanism underlying directed attention to rest and recover. Thereby, nature enhances attentional capacity and the ability to cope and manage life's demands, including coping with illness.

Thus, design intentions are focused on fostering beneficial contact between people and nature in both architectural and urban spaces, by giving importance to features such as natural light, water, vegetation, views of nature, sensory/spatial variability and establishing place-based relationships. In brief, these architecture–nature principles can be summarized in three broad experience categories: (i) nature in the space—which refers to the presence and diversity of natural elements and environmental conditions within the built environment; (ii) natural analogues—which refers to objects, materials and shapes that evoke nature; and (iii) nature of the space—which refers to the spatial configurations resonating with evolutionary human preferences for exploration, mystery and prospect/refuge [94,101].

(iii) Caring disparities

A final aspect of containment of chronic disease concerns the uneven distribution of health, particularly in the USA. Lowincome and ethnic minority populations are more likely than wealthy groups or than 'Whites' to experience a variety of adverse health outcomes, from coronary heart disease to diabetes to chronic bronchitis [102]. The physical places where people live-their houses, their neighbourhood and their workplaces-contribute to the uneven and unequal geographical distribution of health. For example, in the USA, researchers have documented that health-promoting and health-deterring neighbourhood features such as supermarkets, liquor stores and fast food outlets are correlated with race and socio-economic status of communities. Wealthier neighbourhoods are more likely to have supermarkets and gas stations with convenience stores compared to poor neighbourhoods; the same is true of White compared to Black neighbourhoods [103]. Powell et al. [104] found that in Black neighbourhoods, the availability of chain supermarkets was 52% of what it was in White neighbourhoods; differences existed even after controlling for neighbourhood level income [104] (for review, see [105]). A similar pattern is evident with respect to the natural environment, which has well-documented beneficial effects on human health and well-being [95,96]. Nature is often unequally distributed, with disenfranchised populations having less access to natural amenities [106,107]. In New York City, playgrounds in low-income neighbourhoods are more likely, compared to playgrounds in high-income neighbourhoods, to have a variety of hazards including paint chips, trash, rot, rust, splinters and vandalism [108]. Similarly, in Baltimore, Maryland, while Blacks are more likely to live within walking distance of a park, those parks are more likely to be hazardous or polluted, and are typically smaller than those to which Whites have access. So, what do these geographical patterns of health disparities suggest with respect to containment? To most effectively

contain the epidemics of chronic disease that disproportionately affect low-income and minority populations, it is essential to tackle the underlying environmental justice issues, and to distribute healthy, safe, nurturing environments across the population to promote equitable public health.

(d) Containment in animals

Just as space may be used by humans to care for individuals who are at risk of chronic disease, animals too designate locations within their built environments for sensitive individuals. For example, social insects, such as ants and bees, dedicate specific locations within the nest or hive for brood (eggs, larvae and pupae) [77]. Brood can further be moved around the nest to expedite development, for example, by bringing larvae from deep inside the nest to near the soil surface, where it is warm during the day [109–111]. Whether or not animals modify their built spaces to create healthy environments, or to create spaces to care for chronically sick individuals, as humans do, is an open question.

(i) Spatial disparities

Disparity in habitat quality is key in determining population structure and competition in animals. Animals regularly compete over high-quality habitats and defend their territories [112]. Low population densities result in lower competition and better access to resources [113], thus potentially creating more healthy environments in which animals may be less likely to suffer from malnourishment that could lead to chronic stress. The need for shelter can create socially facultative structures in animals that would not be social otherwise. For example, yellow-bellied marmots rely on burrows for wintering and for escaping from predators, thus forming facultative social structures [114]. Interestingly, individuals in larger groups express higher levels of faecal glucocorticoid metabolites, an indicator of stress [115]. Thus, living in a built structure can, in some cases, lead to chronic stress, and dispersing to find a less crowded burrow system might be the best way to contain such chronic stress. Similarly, harvester ant colonies will relocate to new nest sites more frequently in environments with fewer resources compared with areas that have high primary productivity [116]. Thus, changing the built environment, i.e. the nest, by relocating to a new one (instead of restructuring) can potentially help avoid or contain stress induced by low resource availability. Some animals prefer locations that are near conspecifics, for example, to gain better access to mates, and potentially because conspecifics can indicate high habitat quality and be used as cues. Such attraction to high-density areas is known as Alee effects [117,118] and they may facilitate social interactions that can reduce chronic stress, as detailed above.

3. Infectious disease

(a) Prevention in humans

In this section, we consider how the built environment can prevent epidemics and the flow of infectious disease. As noted above, contagious diseases have been the direct cause for changes in the fields of urban planning and architecture since the mid-nineteenth century in the efforts to eradicate the unhealthy living conditions that were believed to support various epidemics. Specifically, the hygienist agenda was embraced in the early twentieth century as one of the postulates of modernism [1,92]. Closely linked with tuberculosis as a medical obsession of the time, modern architecture has produced a specific set of spatial typologies with assumed therapeutic and prevention effects, such as large windows, flat roofs and terraces open to sunlight, air, nature and physical exercise [6,119]. In this sense, modern architecture developed around two kinds of symbolic figures: the 'fragile tuberculosis patient seeking a cure' and the 'athletic figure seeking prevention from the diseases of modernity' [119]. As in the case of chronic diseases, architects and urban designers have historically applied similar strategies for dealing with infectious diseases, whether through prevention or finding ways to contain the epidemics' spread and help alleviate the symptoms once they appear. As with our consideration of chronic disease, we examine the relationship between infectious disease and the built environment and design strategies at several levels, including urban, architectural and small-scale design features within buildings.

(i) Health, indoor environmental control and building materials The legacy of modernist hygienist ideas for prevention of epidemics can be seen in contemporary sanitary approaches to designing indoor environmental climate and in regulations regarding the health effects of various building materials. Environmental factors such as indoor air quality (e.g. air pollution, odours, fresh air supply and ventilation), lighting quality (e.g. view and illuminance), thermal comfort (e.g. moisture and temperature) and acoustical quality (e.g. noise from outside and indoors) are measured and controlled for their effects on the three systems of the human body-the nervous, immune and endocrine systems-through which they influence physical and mental health [120]. To prevent, or reduce, the spread of infectious diseases, contemporary building standards take into account the different modes of disease transmission, including indirect contact with airborne pathogens and contaminated objects, direct person-to-person contact and droplet spread. For example, in the case of airborne viruses, such as influenza, engineering control methods include the careful design of hospital building air cleaning and ventilation (both natural and mechanical). Such measures help dilute airborne pathogens and control their movement between spaces [121]. The role of physical structures in preventing disease spread was highlighted in the 2003 outbreak of SARS (severe acute respiratory syndrome) in a private residential apartment complex in Hong Kong, where the ventilation system and sanitary plumbing expedited the spread of viral aerosols [122,123]. Furthermore, disease can spread through contaminated objects, and the choice of building materials and coatings of indoor surfaces, such as walls, floors and furniture, can decrease the survival of pathogens and ease cleaning and sterilization.

Pollutants originating from toxic substances in building materials, such as heavy metals and asbestos, cause various neurological, cognitive and behavioural disorders and diseases like cancer [46]. Besides 'sick-building' syndrome, there is now a movement toward transparency regarding the chemicals and potentially harmful substances employed in building materials, furniture and finishes within the interior environment. Led by the architecture firm Perkins and Will, the 'Transparency Project' (www.transparency.perkinswill.com) documents substances such as arsenic, phthalates and volatile organic components, and their associated health risks. Moreover, with respect to urban outdoor environments, a recent study of citizens in Barcelona has found a link between urban air pollution and an increase in cases of depression and anxiety [124]. One way to control the pollution of urban air has been through the development of new 'living façade' systems that use plants and other organisms to absorb the pollutants of the city and purify the air [2]. Similarly, with the attentiveness to which species are planted in green areas, urban spaces are being transformed into allergy- and asthma-free environments.

(ii) Small-scale design interventions

In addition to influences on infectious disease at the urban and building scales, in recent years, researchers have begun to consider how smaller design features of buildings, particularly healthcare environments, might deter the spread of infectious disease. Approximately 5-10% of patients in US hospitals acquire an infection while in the hospital, resulting in 99 000 deaths each year [125]. Handwashing is a proven strategy to reduce infection rates and yet medical staff compliance has been elusive. Birnbach *et al.* [126] found that if the hand sanitizer dispenser was directly in the line of vision, in comparison to when the dispenser was adjacent to the doorway (as is quite typical), nearly 55% of physicians sanitized their hands. When the sanitizer was near the doorway, just 11.5% of physicians used it.

(b) Prevention in animals

Various aspects of the built environment can facilitate the prevention of spreading infectious agents. Here, we discuss a number of prevention measures observed in animals: antibacterial or antifungal materials embedded within structures; removing vectors of infection from the built environment; avoiding locations that have been previously exposed to pathogens, or show evidence of harmful consequences to its occupants, and structuring the built environment in a way that reduces interactions that may facilitate disease transmission among individuals.

(i) Building materials

Certain building materials, such as plant parts with antibacterial or antifungal properties, are integrated into animal nests to protect the inhabitants from disease [127]. Wood ants use resin from coniferous trees as nesting material. This resin inhibits the growth of bacteria and fungi and enhances the survival of the nest's inhabitants [128]. Honeybees incorporate resin from plants into the wax that forms their hive, thereby reducing the bees' investment in the expression of immune function genes [129]. Several bird species include green aromatic vegetation in their nest materials to reduce parasite load [130-133] and wood rats place California bay foliage in their nests to reduce the abundance of ectoparasites [134]. Termites line their nest walls with faecal pallets that decrease the germination of fungus spores [135], and certain ant species secrete antimicrobial compounds onto their nest walls to prevent the growth of harmful microbes in the nest [136]. Finally, dry nesting
material used by termites has lower loads of microorganisms compared with damp nesting material [137].

(ii) Removing and avoiding infectious agents

Removing vectors of infection from the nest, such as waste, excretions and dead or sick individuals, is common in animals, especially in social insects. Honeybees and many ant species remove dead individuals from their hive or nest [138–140], a behaviour that extends the lives of the remaining colony members [141]. Ants and bees can detect diseased individuals and behave aggressively towards them [142] until they leave the nest [143]. However, aggression is not always required and, in some ant species, sick individuals will remove themselves from the nest, without interacting with nest-mates [144]. Studies of the mechanisms underlying the 'undertaking' hygienic behaviour in honeybees have revealed complex gene regulation [145] and uncovered which neurotransmitters are associated with this task [146]. Waste is removed from the nest by specific ant workers that do not perform other tasks [147,148] and will not go on to perform other tasks before they die [149]. Interestingly, leaf cutter ant species that live in wet environments will dig special waste chambers inside their nest, while leaf cutter ant species from arid environments will dispose of their waste outside the nest [150]. One potential explanation for this difference is that in wet environments, microorganisms in the waste are more likely to spread and so confining waste in chambers that can be closed off reduces the risk of spreading pathogens. Other sanitary behaviours in animals include the use of latrines to concentrate excretions in one or a few locations inside or outside the nest. For example, all individuals in a colony of social spider mites defaecate in one location, usually near the exit of the nest [151], some ant species concentrate their faeces in certain locations inside the nest [152], and birds remove faecal matter from their nest, especially when there are offspring present [153]. Many mammal species create faecal latrines; however, these are mostly used for communication, rather than for sanitation [154-158].

In addition to removing infectious agents, animals can avoid locations that have either been exposed to pathogens or show evidence of disease. For example, mole crickets change where they dig tunnels to avoid areas where fungi are present [159]. Pathogens may linger in the environment and lead to the spread of disease. Non-synchronous crevice use in the Gidgee skink results in more frequent transmission of pathogens than direct social interactions [160]. Furthermore, the behaviours and habitat preference of the parasites may play a critical role in where they are found and how likely they are to persist inside a host's burrow [161]. Thus, the spatial behaviour of both hosts and parasites can impact the spread of infectious disease. For example, pygmy bluetongue lizards occupy burrows built by spiders and their choice of which burrow to occupy and how frequently to move between burrows can impact their parasite load. Individuals that move frequently between burrows are more likely to encounter and transmit a parasitic nematode [162]. Some animals avoid locations that have signs of infections. For example, great tits avoid nest-boxes with fleas and preferentially select clean nest-boxes [163]. Some ant species avoid areas in a nest with microbes [164] or avoid moving into nests with dead ants when selecting a new nest site

[165]. However, other ant species preferentially choose nest sites with fungi [166], or with dead ants that are visibly infected with fungi [167], over clean, empty nests. It is possible that a low-dose exposure to such pathogens results in immunity during later encounters with it (like a vaccination) [168,169] or that the pathogen is attracting the ants and manipulating them behaviourally to facilitate its spread. Thus, nest selection does not always lead to the avoidance of disease.

(iii) Structure design

Animals may create structures that influence direct interactions that facilitate disease transmission between individuals. For example, creating compartmentalized spaces can segregate the society and allow only subsets of individuals to interact at any given time. Models comparing disease spread in various structures predict that if an infection begins at a single location, it will take longer to reach everyone in a group housed in a compartmentalized structure, compared with a compartment-less structure, in which individuals interact with one another uniformly [16]. However, other models show that spatial structures have only a small impact on disease transmission [170]. Empirical studies that examine the relationship between the built environment, interaction patterns and disease transmission are still lacking. Studies of how population densities influence disease prevalence provide some insights into how built structures may affect disease transmission. For example, ecto-parasite loads decrease with nest density in colonies of bee-eaters [171]. Furthermore, a common argument in the social insect literature is that the high density of social insects inside their nests puts them at risk of rapidly transmitting infectious diseases within the nest. However, such disease spread is seldom seen, leading to the development of many hypotheses about how social insects achieve 'social immunity' [172,173] or 'organizational immunity' [174], including through structuring their nests to regulate interaction rates [174]. For example, small nest entrances protected by guard workers may prevent pathogens from entering the nest [175]. Finally, wildlife managers may take action to prevent the spread of disease, for example through vaccination. However, such management actions can, in fact, expedite the spread of disease by creating unnatural spatial clustering of animals. For example, the use of feeding stations to distribute vaccinations for disease prevention spatially clusters animals and increases the risks of disease transmission [176].

(c) Containment in humans

While epidemic outbreaks of many communicable diseases, like measles and poliomyelitis, have been largely reduced thanks to vaccination and immunization, the complete eradication of infectious pathogens has been limited [177]. One reason for this includes the changes in epidemiological characteristics of infectious diseases due to increasing urbanization. According to Alirol *et al.* [178], higher population density affects the transmission speed of diseases, such as influenza and tuberculosis, that rely on direct contact and proximity. The rural-to-urban migrations and worldwide travel have also led to an increased risk of epidemics whether by introducing new pathogens to the urban environment from adjacent rural areas or because newcomers lack the immunity to certain endemic diseases. The physical environment of cities has either provided or eliminated favourable conditions for many infectious diseases. Unplanned urban expansion, such as slums, has brought about problems of inadequate sanitation, allowing the spread of water-borne diseases and creating breeding sites for various disease vectors, while improved housing conditions and destruction of vector habitats resulted in a decline in infectious diseases in other parts of cities [178]. For example, dengue fever (a mosquito-borne disease) is now found mainly in tropical urban environments. This disease has re-emerged recently due to high population densities, low herd immunity and increased mobility of people, including viremic individuals, leading to broader spatial propagation of the disease within the city [179]. In this section, we discuss the current models for understanding the flow of infectious diseases and strategies for containment of epidemics in urban environments and within buildings.

(i) Disease transmission and spatial configuration

Modelling the dynamics of infectious diseases in human social networks requires looking at three interacting components: the transmission of disease, the flow of information regarding the disease and the spread of human preventive behaviours against the disease [180]. The built environment can have a significant impact on two of these components of epidemics. First, because the diffusion of many infectious diseases is closely linked to the patterns of human mobility and social interaction, it is also directly influenced by the properties of the built environment such as spatial configuration of spaces within the buildings. Second, contemporary disease outbreaks cause a disturbance in the usual everyday functioning of public spaces and city infrastructures. Such changes occur especially when preventive measures (both planned and spontaneous) take place and include emptying streets, fever checkpoints at transportation hubs, forced closures of hospitals and voluntary quarantines [123]. Hence, a major challenge for epidemiology models lies in identifying and mapping the overlap between the social, behavioural and spatial factors that enable the transmission of disease.

Existing models have uncovered several important aspects related to the effects of social interactions and mobility patterns on disease dispersion. Modes of social interaction and of disease spread both impact the number of infected individuals. The nature of social contacts can be close, e.g. individual contacts that happen at home, in workplaces and in social situations with friends, or casual, e.g. occasional contacts at service places. Modes of disease transmission include airborne droplets, contaminated surfaces or direct transmission [181,182]. Importantly, contact networks are heterogeneous, i.e. opportunities for transmission are not equal for all individuals [183,184], but will depend on their spatial and temporal patterns of use and mobility. For example, the daily mobility patterns in developed highdensity urban societies (e.g. journeys to work) are highly predictable. Therefore, public transportation and transfer points are considered 'transmission highways'. City-level models based on integrated traffic information, geo-spatial data and infection dynamics and spreading characteristics allow for developing preventive strategies for particular diseases, like airborne pandemic influenza A (H1N1) [185] and vector-borne malaria influenced both by infected mosquitoes and daily commuters [186]. When the daily routines of inhabitants are irregular, for example in resource-poor

neighbourhoods in Peru, geographical space, economic and social context structure all influence transmission dynamics of an influenza-like pathogen. Less predictable movement patterns corresponded with increased epidemic size [179]. While current epidemiological models generally consider the spatial dimension of disease dispersion [187,188] typically by using new technologies, such as geo-spatial mapping (GIS), Bluetooth, mobile phone tracking and social networks, the exact spatial configuration of the physical environment is not taken into account. As illustrated in previous sections, spatial structures can directly affect social interactions within cities and buildings. A promising approach for incorporating architectural and organizational data into large-scale epidemic forecasting models was proposed by Potter et al. [189]. In their model, they used architectural distances measured between workstations to model contact networks between members of a research institute as directly dependent on the spatial layout of the building.

(ii) Containment strategies through isolation and guarantine

The main aim of disease dynamics models is to identify critical infection points and propose effective mitigation strategies either to prevent disease outbreaks (e.g. through targeted immunization) or to contain epidemics. Control measures that are directly related to the built environment typically involve social distancing and include separation of ill individuals from the rest of the population through spatial clustering, i.e. isolation or quarantine, and closing public places such as schools [181,190,191]. Historically, isolating sick individuals began in the first hospitals, as early as the twelfth century. Similarly, between the mid-nineteenth and mid-twentieth century, there was mass building of sanatoriums, especially for tuberculosis. The architecture of these sanatorium buildings was envisaged with the ease of care and sanitization in mind, with specifically designed furniture and materials. It further included open terraces and large windows as therapy involving exposure to sunlight and air [6,119].

(d) Containment in animals

Containing infectious disease in animals can be achieved by altering social interactions, for example, to facilitate grooming behaviour and remove or avoid diseased individuals. Furthermore, human intervention, for example, in the case of wildlife management and conservation, may impact the containment of infectious disease in animals.

(i) Social interactions

Grooming behaviour is one common method for containing infectious diseases. In addition to reducing stress levels, as discussed above, grooming is commonly used by animals to clean themselves and others in their group of ectoparasites [192–195]. Although grooming behaviour may prevent the spread of ectoparasites, it can facilitate fomite transmission and spread certain infectious diseases, such as tuberculosis [196]. Therefore, self-grooming is more likely to contain a disease and allogrooming is more likely to facilitate disease spread [197]. Furthermore, grooming can be associated with energetic costs, because individuals who are grooming are not resting, eating or watching out for predators [198]. Thus, built structures that can reduce these costs of grooming, for example, by creating food stores and protecting from predators, may promote animal health.

As discussed above, removing diseased or dead individuals from built structures is common in the animal world, especially in social insects. This is similar to quarantine in human societies, where sick individuals are spatially isolated from healthy individuals to contain a disease. Relocating to a new nest site, similar to human evacuations, is another way to contain the spread of infectious agents [199].

More broadly, altering social interaction patterns through modifications to the spaces that animals occupy can change disease dynamics [200]. Theoretical work linking social interactions and disease transmission reveals which interaction patterns expedite disease transfer [201-203]. For example, highly compartmentalized social structures, which can be achieved by living in compartmentalized structures such as nests with chambers, may slow the transmission of disease [204-206]. Experimental work in honeybees provides some information on how spatial organization may affect disease transmission throughout a society. When colonies are exposed to a pathogen for a short time, the disease remains on the outskirts of the nest, but when the colony is exposed to a disease for long periods, the infectious agents can reach the centre of the hive and potentially affect the entire colony [207]. Thus, the structure of the hive or nest can impact the rate at which infectious agents spread and modifications to this structure may aid in the containment of a disease, once it has been introduced. Whether or not animals modify the structures they live in to contain the spread of infectious disease is an open question.

(ii) Human intervention

Containing infectious disease is a special concern for wildlife management and conservation. For example, bat populations have declined substantially due to a fungus causing 'white nose syndrome' [208]. Models for containing the disease take into account the spatial distribution of the caves in which bats sleep to determine the best course of intervention that will have the largest positive impact on the entire population [209]. A large-scale, long-term, containment effort to reduce tuberculosis in cattle in the UK has been to cull badgers, which are a vector for the disease. However, the spatial arrangement of badger populations and the dispersal of healthy individuals into areas where badgers had been culled led to faster spread of the disease instead of its containment [210,211]. Thus, spatial behaviour, such as dispersal, den structure and occupation patterns, should be carefully considered in wildlife management plans aimed at containing infectious diseases [212].

4. Conclusion: the effects of the built environment on disease and health behaviours in both humans and animals

In our review of the literature to identify how the built environment might impact disease and health behaviour in both humans and animals, we identified parallels and differences between human and non-human animal societies that may provide a basis for expanding our knowledge of both.

Many chronic diseases in both animals and humans emerge from heightened stress. The built environment may facilitate the reduction of stress by changing social interactions. However, not all animals require the same amount of social interaction to reduce stress. Crowding in humans can induce stress and depression, but so can complete isolation. Animal species differ in the amount of social interactions they require: highly social species require frequent interactions, whereas many social interactions increase the stress in facultatively social species. Thus, the amount of social interactions facilitated by the built environment should fit the social structure and preferences of the species occupying the built structures. Feedback between social processes and built structures can further influence their effect on health behaviours. These social processes differ between humans and animals and among social situations, thus raising the importance of considering social processes and built structures in tandem. Future theoretical work on the amount of social interactions that various structures facilitate may help prevent and contain chronic diseases that stem from heightened stress in a wide range of species, including humans, highly social non-human animal species and solitary species.

In some cases, we found opposite impacts of built structures on human and animal health. For example, physical activity promotes health and longevity in humans, but in animals, we see the largest within-species longevity differences between individuals that are completely sedentary, protected by their built environment and living to old age (social insect queens), and those that are extremely active and die relatively young (social insect workers). Similarly, built environments that create easy access to energy-rich foods (such as sugars and fats) benefit animals but harm humans. This difference likely stems from the agricultural and industrial revolutions that have enabled humans to produce food in excess and escape the 'Malthusian trap'.

Hygienic behaviours are used by both humans and animals to prevent the transmission of infectious agents. Both humans and animals use certain building materials that promote health. Humans may be inspired by some of the materials that animals use and incorporate those into their buildings, or cleaning supplies, using biomimicry to prevent the growth of microorganisms where they are not wanted. Both humans and animals engage in sanitary behaviourwhether it is hand washing in humans or removing infectious agents in animals. Perhaps studies on where hand sanitizers are positioned in hospitals can inform studies of sanitation behaviour in animals. For example, these studies may guide researchers seeking locations that promote sanitary behaviours in wild animals and inform the configuration of animal enclosures for captive animals in zoos and biomedical research facilities, to facilitate sanitary behaviours, such as grooming.

Modifying how spaces are used can prevent and contain infectious disease in both humans and animals. Isolation and quarantine are common in human societies, similar to the removal of infectious agents, dead or diseased individuals, in animals. Evacuation of areas where epidemics are spreading rapidly can be a way to contain infectious disease in humans, similar to nest evacuations in animals. Furthermore, animals may use spaces infected with low doses of microbes to gain immunity, similar to vaccination in humans. Modelling how individuals move in different spaces and how these movements influence interactions that may lead to disease transmission, using social network analysis, can improve our understanding of the effects of the built environment on disease transmission in both humans and animals.

In both animals and humans, restructuring the built environment can reduce or prevent disease transmission. However, little is known about whether such changes are, in fact, made. The built structures we discuss can be constructed by the individuals who occupy them, by other individuals from the same species or by other species. Regarding animals, we discuss both the structures that the animals build themselves and structures that humans build for them-for example, in zoos, agriculture and the laboratory. Humans often occupy spaces that others have designed and built for them. Considering who designs and constructs the built environment is fundamental for understanding whether and how it can be modified in response to various conditions, such as chronic and infectious diseases. For example, in humans, many agencies may be involved in permitting the re-modelling of spaces, which may slow down the changes. Whether animals modify the structures they build and occupy in response to disease is still an open question. This open question can be examined in animal systems using experimental manipulations that might not be feasible to conduct in humans, but may inform both human building designs and our understanding of animal behaviours.

The impact of global climate change (GCC) will have a variety of effects on the health of both humans and animals [213-215]. While some of these impacts are predictable, others cannot yet be forecast. As sea levels and temperatures rise, humans will be increasingly faced with drought, floods, natural disasters and consequent relocation and migration to new regions. As temperatures rise, physical activity may be less possible in some places but more viable in others [216]. In addition, the distribution of animal and human disease vectors will likely be affected by rising temperatures. For example, increase in mosquito populations and changes in their spatial distribution may increase rates of malaria and affect unprepared populations [217]. Human migration in response to sea-level rise and natural disasters could further change global disease transmission dynamics. Animal health will also be impacted by GCC, for example, through changes in distribution ranges that will expose animals to new areas with potentially different pathogens or increased temperatures that will increase the range of pathogens and/ or their persistence in the environment.

New digital and communication technologies that are increasingly infusing the built environment, such as the 'Internet of Things', virtual reality, mobile communication devices and cloud servers, are becoming indispensable in understanding and monitoring health issues in both humans and animals. For example, individual health tracking devices are increasingly used to gather physiological and psychological data to monitor individuals' general health or specific chronic conditions [218,219]. Various smart sensors are currently used to improve the quality of indoor environments by gathering data on people's comfort needs and behaviour, both at the individual and at the social scales [183,220,221]. These tracking systems will likely be used in the future to develop personalized treatments and can contribute to the investigation of the effects of physical and social environments on health outcomes. Similarly, epidemiological models could benefit from combining information on spatial, social and behavioural factors when modelling disease transmission within human and/ or animal populations separately, or in cases of zoonosis outbreaks [222]. Novel technologies like virtual reality are also being explored for their possible application for therapeutic purposes, such as restorative effects of being virtually immersed in natural settings [223]. The cybersphere may have multiple beneficial contributions for understanding the underlying causes of health conditions in humans and non-human animals.

We have discussed many ways in which humans and animals interact through built structures: for example, humans build structures to keep animals in zoos, farms and laboratories; cities have become part of the habitat of many animals and humans modify animal spaces as part of conservation actions. One important interaction between humans and animals that can be mediated by the built environment is the propagation of zoonotic disease. Such interactions have led to zoning of cities, as we detailed at the beginning of the paper. However, zoonotic diseases are still prevalent around the world and present an ongoing public health concern because their emergence is tightly connected to urbanization processes, global travel and trade routes, and changes to ecosystems and biodiversity [178,224]. All these changes have opened new disease transmission pathways between humans, domestic animals and wildlife and are fuelling multi-disciplinary approaches to control and prevent infectious diseases. Therefore, epidemiological models would benefit from insights into the impact of the physical environment on the prevention and containment of both infectious and chronic diseases. For example, understanding the effects of urbanization on human and non-human animal systems can offer new ways to predict the emergence of novel diseases and new methods to control endemic zoonoses in developing countries and unplanned fast-growing city areas. Interestingly, the implementation of health-promoting design strategies to reduce chronic disease in humans, such as providing green spaces in cities, has led to an increase in biodiversity and in controlling potential zoonotic diseases. One way to examine the links between human and animal activities and how they affect disease dynamics has been through the development of human and animal health information systems, which collect spatial disease data at regional and national scales [225]. Further work is needed to develop models of disease epidemics, especially for crossing boundaries between human and animals and across geographical space. Such models will require information on zoonotic disease, host and vector-borne transmission, and movement patterns of both humans and animals. Thus, in-depth understanding of how interaction patterns depend on the built environment would greatly contribute to developing spatial models of infectious disease transmission through social mixing networks, both within and across species.

Overall, infectious and chronic diseases in humans and non-human animals need to be understood as a worldwide public health concern, given the largely anthropogenic drivers such as the built environment behind many diseases. Accordingly, securing the health and well-being of all living social systems requires holistic and mutually informed understanding and development of prevention strategies at local, regional and global levels.

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The architecture of *network collective intelligence*: correlations between social network structure, spatial layout and prestige outcomes in an office

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A social network represents interactions and knowledge that transcend the intelligence of any of its individual members. In this study, I examine the correlations between this network collective intelligence, spatial layout, and prestige or status outcomes at the individual and team levels in an organization. I propose that spatially influenced social cognition shapes which individuals become members of prestigious teams in organizations, and the prestige perception of teams by others in the organization. Prestige is a pathway to social rank, influence and upward mobility for individuals in organizations. For groups, perceived prestige of work teams is related to how team members identify with the group and with their collaborative behaviours. Prestige enhances a team's survivability and its access to resources. At the individual level, I ran two-stage Heckman sample selection models to examine the correlation between social network position and the number of prestigious projects a person is a member of, contingent on the association between physical space and social ties and networks. At the team level, I used linear regressions to examine the relationship among network structure, spatial proximity and the perceived prestige or innovativeness of a project team. In line with my hypotheses, for individuals there is a significant correlation between physical space and social networks, and contingent on that, between social network positions and the number of prestigious projects that a person is a member of. Also in accordance with my hypotheses, for teams there is a significant correlation between network structure and spatial proximity, and perceived prestige. While cross-sectional, the study findings illustrate the importance of considering the spatial domain in examinations of how network collective intelligence is related to organizational outcomes at the individual and team levels.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

Interpersonal interaction and collaboration are key ingredients for individual and team thriving in social groupings including organizations. This is not a recent phenomenon. In fact, there are remarkable similarities between groups as diverse as hunter–gatherer bands [1] and work teams and organizations [2] with respect to dependence on their members' ability to collaboratively identify and exploit resources critical to individual and group outcomes. Cognition plays a major role in this process. Importantly, cognition is not merely confined to social knowledge, but also includes knowledge of physical space. More precisely, spatial cognition shapes social or socially shared cognition, which is, in turn, constituted by interactions among individuals [3,4]. Understanding socially shared cognition requires an analytic focus on the group's pattern of social interactions, its social

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Figure 1. Relationship between social networks, space and (*a*) identification of expertise in individuals and (*b*) perception of a project team as prestigious and innovative. These relationships are actualized via social cognition, which is itself influenced by spatial cognition of the physical space or architecture. (Online version in colour.)

network. The social network represents interactions and knowledge that transcend the intelligence of any of its individual members [5]. In this study, I examine the correlations between this *network collective intelligence*, spatial layout, and prestige or status outcomes at the individual and team levels in an organization.

I propose that spatially influenced social cognition shapes which individuals become members of teams in organizations, and how teams are perceived by others in the organization. I define the organization as a group of groups, where individuals and groups have to compete for the scarce resources that are critical to success and survival [6]. The pursuit of status and prestige are part of this competition and are universal to all social groupings including status hierarchies such as organizations [7,8]. Expectations state theory predicts the emergence of status hierarchies under conditions of task orientation (individuals motivated to solve a problem) and collective orientation (consideration of others' contributions in task completion) [9]. Prestige represents a strategy or pathway to navigating these hierarchies and to status acquisition [10]. For individuals within groups, the concept of prestige captures the cognitions, behaviours and emotions aimed at status attainment through displays of skill and knowledge [10-12]. Prestige is a pathway to social rank, influence and upward mobility for individuals in organizations [12,13]. For groups, research has shown that the perceived prestige of work teams is related to how team members identify with the group and with their collaborative behaviours [14,15]. Prestige enhances a team's survivability and its access to resources. For example, a project team that is perceived to be prestigious and innovative is likely to have higher levels of external contact and communication with other individuals and groups in the organization [16]. This communication is central to how team members seek information, resources and support within the organization [17].

Interactions within social networks facilitate social cognition about which individuals have what ability or expertise. The theory of transactive memory proposes that, by communicating and interacting in networks, group members are able to identify and leverage the skills and expertise of others in the group [18]. Socially shared cognition, the collaboration among group members as they collectively encode, interpret and recall information [19], is thus a function of the social network. By interacting, individuals identify expertise in others that can be leveraged in projects critical to the organization's survival. But once these projects acquire the human resources with the requisite skill sets needed to ensure their success, then this feeds into the social cognition that informs the perceived prestige of project teams in the organization. This is the process captured by the framework in figure 1. I also examine whether networks are correlated with the composition of teams that are perceived as prestigious and innovative by organizational insiders. I hypothesize that an individual's place in the organization's social network structure plays a role in their membership in teams with high prestige, which has positive benefits for an individual's sense of self and career [14,15]. Where as prior research focused on the link from perceived prestige to group performance, in this study, I examine the association between: (i) network centrality, spatial layout and the frequency with which an individual is a member of prestigious project teams and (ii) the association between the perceived prestige of a project team, and the group's network structure and collective spatial proximity. Note that while the framework suggests that physical space impacts prestige through its effects on social networks, it also allows for the association between social networks and individuals' spatial assignment and location.

A social network is the pattern of relations and interactions among the individuals in a group. Moreover, the network has resources—which are sometimes referred to as *social capital* that individuals can access and use [20,21]. Network position leads to individual differences in social capital. However, the social network is also a collective intelligence where the group whole is greater than the sum of individual intelligences [22]. My discussion of spatial and social cognition notwithstanding, I conceptualize 'collective intelligence' in network rather than in cognitive terms. In fact, I argue that the connectedness and immersion of humans in social networks means that collective decisions can be understood even if they are not declared explicitly [5]. However, I also acknowledge that physical space plays a significant role in the creation, maintenance and death of social ties and networks [23-25]. A key mechanism behind the influence of space on social networks is the structuring of face-to-face interpersonal encounters and interactions. Faceto-face (as opposed to electronically mediated) communication and encounters rely on the latent potential of physical space to structure potential encounters, which is contingent on the co-location of individuals.

The spatial layout can hinder or enhance the formation of social ties and networks, the operative mechanism being the impact of spatial cognition on social or socially shared cognition. This type of spatially influenced social cognition shapes the group networks that are formed via interactions between individuals. Moreover, individuals and groups experience the networks and physical space as structures of constraints and opportunities that are associated with individual and group outcomes. My thesis is that conceptualizing how social networks operate or function in physical space allows better understanding of the effects of network structure on individual and group outcomes. Next, I will review the research on spatial cognition, and socially shared cognition and social networks.

(a) Spatial cognition

An individual's knowledge of the world is first experienced through the body and the spatial world that the person inhabits and interacts with [26]. Cognition, perception and action are shaped by the movement and interaction of our bodies in the physical environment [27]. Spatial cognition refers to various aspects of cognitive processing such as spatial: perception, memory and navigation or wayfinding [28]. Spatial cognition operates at multiple scales ranging from the space: of the body, around the body, of navigation and of external representations [29]. The space of the body has both perceptual (external and internal sensations) and behavioural (what the body does) dimensions [29]. The space around the body is the space of what we can immediately affect, as well as what immediately affects us [29]. The space of navigation or potential travel is the space of how we move around in buildings, cities and natural landscapes. Space is stitched together experientially, perceptually, from actual navigation, or cognitively via maps or descriptions [29]. Lastly, the space of external representations is created by people to aid cognition, such as the use of maps or architectural drawings to represent actual spaces [29]. I focus on the impacts of networks on individuals and teams confined to the spatial layout of an office floor, privileging the space of navigation and space around the body.

With respect to my thesis, spatial cognition is also inextricably intertwined with, and influences socially shared cognition. Not only do group members need to know who knows what and who is good at what, but they also need to know who is where. Spatially influenced social cognition confers advantages to individuals; those with more of it better know who is where in the organization's physical space.

(b) Socially shared cognition and social networks

Socially shared cognition refers to the process by which individuals in groups collaboratively acquire, encode, store, interpret, recall, transmit and use information in the creation of a collective intellectual outcome [19,30]. The interactions among the individuals, the social network, create a structure that impacts the patterns of communication and distribution of information among the group members. This has appreciable impacts on the group's intellectual potential or collective intelligence. Analysing interactions is key to understanding social cognition [4]. Therefore, understanding the group's social network should yield insights into its collective intelligence. By their actions and interactions, individuals create the interconnections that structure the group's network.

Social network structure places some individuals in more or less advantageous positions compared with others. Individual network position is correlated with access to and potential for exploiting social capital, or network resources [31], and the prominence or visibility of the node in the network. In a knowledge-based workplace, the organizational network typically comprises individuals and teams in a multi-team membership web of relations [32]. Therefore, in addition to analysing the associations between individual prominence in the network and prestigious project membership, I also assess the relationship between network structure and the prestige perception of the project team at the group level. As all individuals in this study are simultaneously members of multiple prestigious and non-prestigious projects, my analysis plan enables me to identify whether network structure is associated with: (i) prestigious team membership for individuals and (ii) perception as 'prestigious' for project teams. With respect to my thesis, individual actions and interpersonal interactions result in a network that, in turn, becomes a source of constraints and opportunities for individuals and groups. Understanding the social network thus simultaneously reveals insights on how network structure shapes individual- and team-level outcomes in organizations [5].

2. Material and methods

(a) Study sample and data description

I administered an online sociometric survey in 2009 to a sample of 37 scientists and engineers who were employees of BRX, a unit responsible for environmental policy and compliance at a large manufacturing firm headquartered in the Midwest of the USA. The survey enabled me to collect data on multiple social networks including interaction, advice-seeking and advice-giving. In addition, I procured internal data on (i) sample attributes, e.g. gender, education and hierarchical or job status, (ii) AutoCAD® drawing interchange (DXF) files of the workplace floor plan (figure 2), and (iii) information on the project team that individuals were affiliated with (N = 30) including an evaluation by organizational insiders on whether the project is prestigious and innovative. The organization was characterized by multiple team membership for individual employees. Excluding the director, who was nominally a member of all project teams, individuals at the organization were involved in a range of 0-21 project teams (mean = 6.56, median = 5, s.d. = 5.51). The project teams had a range of 4-15 members (mean = 8.8, median = 8, s.d. = 2.83).



Figure 2. Floor plan for the study research site. The locations of the individuals in the study sample are indicated using the darkened circles/work chairs. One individual was frequently away at other sites belonging to the parent firm and would use any available workspace when on-site depending on meeting or work schedules. Therefore, this individual is not mapped on the floor plan. (Online version in colour.)

(b) Description of variables and order of analysis (i) Individual level

The perceived prestige of a team augments group identification, which is in turn correlated with collaboration and interaction among team members [14,15]. The thrust of this study is to analyse whether there is a relationship between an individual's position in the network structure, spatial layout and the number of prestigious and innovative project teams that the individual is part of. I created the count dependent variable 'number of prestigious /innovative projects' that captured the number of prestigious project teams that the individual was a member of.

I used the interaction network item from the organizational sociometric survey to generate the social network measures of degree (related to the number of other individuals in the network that the person is directly connected to) and betweenness (how often a person is on the shortest paths between other pairs of individuals). Specifically, respondents were asked 'About HOW OFTEN do you have discussions with this person to get your work done?' The response options were: (i) 1 =monthly or less, (ii) 2 = several times a month, (iii) 3 = several times a week, (iv) 4 = daily and (v) 5 = several times a day. The degree measureindicates individuals that are prominent locally (immediate network neighbourhood). I binarized the degree measure at its median value to create the dependent variable 'degree' that was the outcome in the probit selection equation of the Heckman model (more details in the next section). The betweenness measure identifies individuals that are prominent globally (across the entire network). I used the betweenness measure to create the independent variable 'betweenness'.

The spatial layout measure *integration* (the average depth of a space relative to all other spaces in the system) enables us to capture the ease with which a person can physically access other individuals at the workplace. The measure is grounded in 'space syntax', a theoretical perspective and set of methods that allow the conceptualization and analysis of physical space in

Table 1. Summary statistics for individual-level variables.

variable	n	mean	s.d.	min.	max.
number of prestigious/innovative projects	37	1.3514	1.6024	0	6
degree	34	0.4412	0.5040	0	1
betweenness	34	1.1748	3.3622	0	15.226
integration	37	0.4111	0.0491	0.36	0.57
gender	37	0.5676	0.5022	0	1
graduate degree	37	0.5946	0.4977	0	1
manager	37	0.2432	0.4350	0	1

network terms [33,34]. The measure was generated from a spatial network of the workplace created using the DXF files and DEPTHMAP[®] software. Spaces in this type of network are connected if they are adjacent and directly accessible from each other, i.e. it is physically possible to get from one space to the other. I used the integration measure to create the independent variable 'integration'. Lastly, I created the control variables 'gender' (0 = female, 1 = male), 'manager' (0 = staff/nonmanager, 1 = manager) and 'graduate degree' (0 = Bachelor's or lower, 1 = Master's or higher). Table 1 summarizes the individual-level variables.

(ii) Group level

I worked with management to evaluate whether the organization's project teams (N = 30) were perceived to be prestigious and innovative (n = 6), or not (n = 24). My informants considered

Table 2. Summary statistics for group-level variables.

variable	n	mean	s.d.	min.	max.
size-weighted project prestige/innovativeness	30	0.1532	0.0785	0.067	0.400
interaction network, in-degree centralization	30	0.0414	0.0103	0.030	0.085
spatial distance, average weighted degree	30	857.3571	323.2310	294.667	1469.989

both external (for example, media or press coverage) and internal (for example, how they thought the project was perceived by executives from the parent firm) factors in evaluating whether a project was prestigious and innovative. I also wanted to control for the fact that project teams may vary with respect to the resources that are available, including human capital. Research has shown that while larger project teams have greater human resource capital, thereby enabling them to complete some tasks faster, there are also significant drawbacks to increasing a team's size [35]. Other work suggests that larger teams are more likely to reflect political and bureaucratic interests (such as a maximal head count to ensure representation of all stakeholders) rather than efficiency concerns [36]. I created the group-level dependent variable 'size-weighted project prestige/innovativeness' as follows:

size-weighted project prestige

$$= \frac{\text{(is project prestigious?)} + 1}{\text{(number of individuals in project)}}.$$
 (2.1)

This variable controls for the possibility that resources, including human capital, might be shared unequally across teams and in favour of larger projects, positively skewing these teams' collective intelligence, and thus making it more likely that they are perceived as prestigious and innovative.

I used project team memberships to compute the grouplevel network variables. All 37 individuals in the sample had multi-team project memberships. Using the organizational interaction network, I extracted a subgraph for each project team. For each subgraph or team interaction network (N = 30), the independent variable 'interaction network, in-degree centralization' was generated by computing the centralization measures for the team interaction networks. Centralization captures the extent to which power and other positional advantages are distributed unequally in the network. The most unequal network has a star shape with the nodes on the periphery only having direct connections to the node in the centre. Network centralization informs on the variability of the distribution of positional advantages in a network relative to a star network of the same size (number of nodes or individuals in the present case). For the purposes of this study, centralization indicates the extent to which interactions among team members are concentrated in only a few of them as opposed to being distributed equally across the team [37].

Finally, I computed the *average weighted degree* of the spatial distances which is the average of the sum of weights of the edges, or in this case the distances among individuals in the team. This independent variable was created by generating a network from the matrix of distances among project members. In the spatial matrix, the edge's weight is the metric distance between individuals in a dyad or pair. Therefore the 'spatial distance, average weighted degree' is a function of the number of other individuals that person is connected to, and the distances from the focal individual to the other individuals. The measure thus indicates the overall spatial proximity within a team, while accounting for the team's size.

A key difference between edges in the interaction network and spatial distance matrix is that the former is directed (ties are directional, they can go *out* from the individual or *in* to the individual) while the latter are undirected (ties are bidirectional, or they simultaneously go to and from the individual). For the interaction networks, I computed 'interaction network, in-degree centralization' using *in-degree* or incoming ties as individuals that receive many ties are seen as prominent or high in prestige [38]. Table 2 is a summary of the group-level variables.

(c) Statistical analyses

(i) Individual level

I tested whether the multiple team membership of individuals violated the assumptions of independence in the data sufficiently to merit a multilevel modelling approach (with teams as a nesting variable) over a single-level model with no team effects. I fitted multilevel mixed effects linear and Poisson models with 'number of prestigious/innovative projects' as the outcome. The multilevel linear model had empty random-effects equations, meaning that the single-level linear model with no project team effects was a better fit for the data than the multilevel model. In other words, there was no nesting by the project team. Similarly, the multilevel Poisson model was not a better fit for the data than the single-level model with no project team effects. Therefore, I examined the extent to which network structure and spatial layout were associated with membership in prestigious and innovative project teams using Heckman sample selection regression models, and did sensitivity analysis using the multilevel mixed effects Poisson models. I ran the Heckman model to account for the fact that the theoretical framework (figure 1) assumes that in interacting and collaborating individuals identify expertise in others and form perceptions on the prestige of project teams through social cognition. Spatial cognition plays a role in how individuals navigate the physical space of the organization, which is related to the formation and maintenance of social ties and networks. Thus, the correlation between network structure and prestige outcomes is contingent on the association between spatial cognition and social networks. The Heckman sample selection model consists of two equations: a probit selection equation to model the likelihood that an individual will have a higher than median degree (centrality in the network based on number of ties), and, contingent on this, a linear outcome equation to model the number of prestigious and innovative projects that an individual is a member of.

The Heckman outcome equation was specified as follows. With 'number of prestigious/innovative projects' as the dependent variable, I fitted a model with 'betweenness' as the independent variable controlling for 'gender', 'graduate degree', and 'manager'. For the Heckman selection equation, the dependent variable was 'degree' and the independent variable was 'integration'.

The multilevel mixed effects Poisson model was specified similarly to both Heckman equations with 'number of prestigious/ innovative projects' as the dependent variable, both social network measures ('betweenness' and 'degree') and spatial location ('integration') as the independent variables, and the 'gender', 'graduate degree', and 'manager' controls.

(ii) Group level

I examined the relation between network structure, spatial proximity, and the perceived prestige or innovativeness of a project team using linear regression. I ran a model with 'size-weighted project prestige/innovativeness' as the dependent variable, and

'interaction network, in-degree centralization' and 'spatial distance, average weighted degree' as the independent variables.

(d) Hypotheses

I examined the proposition that there is a correlation between social network structure, physical space or architecture, and (i) at the individual level, membership in prestigious projects, and (ii) at the group or team level, whether a project team is perceived as prestigious and innovative.

A person's location in the spatial system may impact whom they interact with on a regular basis, and the frequency of this interaction. The 'integration' variable captures the average depth of a space from all other spaces in the system. Individuals in spaces with higher integration will be more reachable by others in the organization compared with those in less integrated spaces. Similarly, individuals in more integrated spaces can access others in the organization more easily than those in more segregated spaces. Previous research has indicated that the greater the distance between two individuals, the lower the likelihood of a social relation between them [25]. Extrapolating from dyadic ties to relations among individuals in an organization, then, I would expect that a person who is on average a shorter depth or distance from others would have more social ties, which is captured by degree centrality. Recall that degree informs us that individuals with more ties or connections to others tend to be in favoured positions. I hypothesized that:

H1: Individuals with higher integration will have higher degree.

Social network centrality for individuals captures the extent to which they are in more or less favoured positions compared with others in the network. Being in a favoured position means that someone has fewer constraints and more opportunities compared with others. Network centrality identifies different ways in which individuals have unequal access to prestige or status in the organization. Specifically, 'betweenness' describes how individuals that are frequently on the shortest paths between others in the network are in favoured positions. This dimension of the *network* or *collective intelligence* in the organization should be correlated with the processes associated with individuals' selection into prestigious projects. I hypothesized that:

H2: Individuals with higher betweenness will have higher membership in prestigious projects.

The social network structure of a project team is a function of its individual members, their attributes, and the interactions among its members. There is mixed evidence for centralization and team outcomes. Some studies have found that centralization facilitates team performance [39] while others have found that the opposite is true [40]. Part of the reason for this discrepancy is that the teams studied have been in very divergent contexts with a focus on different types of outcomes, for example, student teams at a business school, professional soccer teams, etc. With respect to whether a team is perceived as prestigious and innovative, moderate to high levels of centralization are more likely to make a project team identifiable with one or a few key individuals that are high in prestige or status. This is likely to result in the team being perceived as prestigious relative to projects with a more equal distribution of connections, or lower centralization, which implies a lower likelihood of identification of the team with any one person regardless of their prestige or status. Specifically, I hypothesized that:

H3: Project teams with higher 'interaction network, in-degree centralization' are more likely to be perceived as prestigious.

Greater spatial proximity within a team would facilitate collaborative behaviours among its members [25], including the innovative collaborations [24], which should be correlated with

a team's prestige perception. The team's 'spatial distance, average weighted degree' is a good indicator of the potential coordination and collaboration costs to a team as a result of how close or far apart team members are, taking into account the number of individuals in the team. For an individual in a team, in terms of spatial costs, walking to the workspaces for three other team members that are each located 10 feet away would be equivalent to walking to the workspace for one team member that is 30 feet away. Lower distances among team members, and hence lower *average weighted degree* should be correlated with greater ease of communication, coordination and collaboration (assuming face-to-face and not electronically mediated communication). Therefore, I hypothesized that:

H4: Project teams with a lower 'spatial distance, average weighted degree' are more likely to be perceived as prestigious.

3. Results

(a) Individual level

With respect to the Heckman selection equation, 'integration' is positively and significantly correlated with 'degree', suggesting an association between spatial layout and social ties and networks. I cannot ascertain causality given the cross-sectional nature of the data. Nonetheless, the results align with the theoretical framework, which posits a link between physical space and social networks (figure 1). The results support hypothesis H1; there is a positive and significant correlation between 'integration' and 'degree'. I did a sensitivity analysis (not shown) for the Heckman selection equation using single-level and multilevel logit regressions with the binarized 'degree' as the dependent variable, and single-level and multilevel linear regressions with raw degree as the dependent variable. The sensitivity analysis confirms the findings on H1. For example, the single-level linear model (model statistics: F = 5.91, p = 0.0208, $R^2 = 0.1560$, n = 34) shows that a unit increase in 'integration' is associated with a roughly 69 unit increase in *degree* centrality (p = 0.021).

With respect to the Heckman outcome equation ('number of prestigious/innovative projects'), social network position ('betweenness') is significantly correlated with the number of prestigious projects an individual is a member of, contingent on the relationship between spatial layout and number of social ties (selection equation). The results support hypothesis H2; individuals with higher 'betweenness' have higher membership in prestigious projects. I did a sensitivity analysis using multilevel mixed effects Poisson models (table 3), and the results support H2. Lastly, table 3 also reports the results of a likelihood ratio (LR) test which compares the multilevel model to a single-level model with no team effects (that is, a linear regression). The LR test statistic 'chibar2(01)' has a value of 0 with a p-value of 1, meaning that the single-level model offers a significantly better fit to the data than the multiple membership or multilevel model.

With respect to the controls, having a graduate degree and being a manager are both significantly correlated with the number of prestigious projects that an individual is a member of (table 4). However, there is no significant correlation between 'gender' and number of prestigious projects.

(b) Group level

The 'interaction network, in-degree centralization' is positively and significantly correlated with 'size-weighted project prestige/innovativeness' (table 5). The 'spatial distance, average

Table 3. Individual-level multilevel or multiple membership Poisson model for 'number of prestigious/innovative projects' (model statistics: Wald $\chi^2 = 245.09$, p = 0.0000, n = 264, groups = 30; LR test versus Poisson regression with no team effects, $\bar{\chi}_1^2 = 0.00$, p = 1.0000).

predictor	estimate	s.e.	<i>p</i> -value
intercept	-2.3865	0.3052	0.0000
betweenness	0.0242	0.0094	0.0097
integration	5.7680	0.7279	0.0000
gender	-0.1520	0.0958	0.1127
graduate degree	0.4128	0.1224	0.0007
manager	0.9934	0.0966	0.0000

Table 4. Individual-level Heckman model for 'number of prestigious/ innovative projects' (outcome equation) contingent on 'degree' (selection equation). Model statistics: Wald $\chi^2 = 4.21 \times 10^8$, p = 0.0000, n = 34.

predictor	estimate	s.e.	<i>p</i> -value		
outcome equation: $DV = 'number of prestigious/innovative projects'$					
intercept	1.1139	0.3696	0.0026		
betweenness	0.0701	0.0334	0.0356		
gender	-0.6041	0.4288	0.1589		
graduate degree	1.2321	0.2004	0.0000		
manager	2.5616	0.4014	0.0000		
selection equation: D\	I = 'degree'				
intercept	- 5.9466	1.2742	0.0000		
integration	13.8341	3.1944	0.0000		

Table 5. Group-level model output for 'size-weighted project prestige/ innovativeness' (model statistics: F = 13.13, p = 0.0001, $R^2 = 0.4931$, n = 30).

predictor	estimate	s.e.	<i>p</i> -value
intercept	0.1711	0.0583	0.0067
interaction network,	2.4233	1.0655	0.0311
in-degree centralization			
spatial distance, average	-0.0001	0.0000	0.0004
weighted degree			

weighted degree' among the project members is negatively and significantly correlated with the 'size-weighted project prestige/ innovativeness'. The results support H3; there is a positive and significant correlation between 'interaction network, in-degree centralization' and a project team being perceived as prestigious. The results also support H4; there is a significant correlation between teams having a lower 'spatial distance, average weighted degree', and their perceived prestige (table 5).

4. Discussion

In this paper, I evaluated the individual- and group-level associations of *network collective intelligence* and physical space

with prestige. I found that for individuals, as hypothesized, there is a significant correlation between physical space and social networks, and contingent on that, between network position and prestige. For project teams, I found that in accordance with my hypotheses there is a significant correlation between network structure and spatial proximity, and prestige.

For individuals, being located in a space that is easily accessible to and from all other spaces in the workplace is correlated with having more social ties in the organization. This finding is aligned with Zipf's Principle of Least Effort [41], which postulates that, all other factors being constant, people will choose the path of least resistance or effort. Therefore, if it is easier for people to find you physically, then they may be more likely to make the effort to contact you in the context of faceto-face interaction, and hence the significant correlation with the number of social ties that you may have. Previous work has established that spatial proximity is a greater determinant of social interaction than sociodemographic factors, such as common interests and family background [42]. Proximity has also been shown to amplify factors that are conducive to tie formation, including social similarity [43]. My results illustrate the importance of considering the spatial domain in examinations of how network collective intelligence is related to organizational outcomes.

I also found that, contingent on the social ties that you have, 'betweenness' network centrality-which captures a person's importance across the whole network-is positively and significantly correlated with the number of prestigious and innovative projects that the person is involved with. Individuals that are high in 'betweenness' are thought to have advantages with respect to obtaining novel information and other resources from disparate parts of the network. Previous studies have found a positive relationship between an individual's 'betweenness' and their perceived centrality by senior management [44]. Potentially, the increased visibility that is associated with individuals that have high 'betweenness' may explain not only why their expertise is more likely to be identified or recognized, but also why they are more likely to be placed in prestigious and innovative projects. The study findings suggest that an individual is more likely to be involved with prestigious projects when the focal person is frequently on the shortest paths between other pairs of individuals in the organization.

At the group level, 'interaction network, in-degree centralization' or the distribution of network ties is positively and significantly correlated with the team's prestige, suggesting that some centralization in a group may be useful. Recall that centralization is a network-level measure that captures how dispersed or concentrated individual centralities or positional advantages are in the network. Previous longitudinal research has established that moderate centralization facilitates team performance as evaluated by experts [39]. In a knowledgebased workplace, there may be no clear-cut path to desirable organizational outcomes. Thus, there may be a level of uncertainty about the performances of others, and even technological uncertainty [45]. This uncertainty may make a person that is high in prestige or status a desirable collaboration partner as others in the organization are more likely to infer expected performance from perceived prestige or status [45]. Equally or even more likely, project teams may be formed around individuals with high levels of expertise (and hence high prestige) in the subject matter that is pertinent to the project. These individuals may either select or attract other

individuals who may not have similarly high subject matter expertise (hence low prestige) but who may have other complementary skills that are essential to the success of the team. I do not have the data to ascertain which mechanism drives the process that results in the significant correlation between 'interaction network, in-degree centralization' and a team's perceived prestige. However, it is logical to conclude that pairing high-prestige individuals to others with lower prestige would lead to project teams with high 'interaction network, indegree centralization'. The association of the team with the high prestige individual may very well confer prestige and status to the individual's team in a climate of uncertainty about organizational outcomes.

The 'spatial distance, average weighted degree' is negatively and significantly correlated with a project team's prestige and innovativeness. Specifically, teams with a lower average weighted degree are perceived as more prestigious and innovative. Simply put, co-location and distance matter [46]. Not only may teams with a lower 'spatial distance, average weighted degree' provide more opportunities for the encounters that enhance collaborative behaviours, but the reduced spatial costs of faceto-face communications among team members may correlate to higher impact outputs [47]. After all, there are characteristics of face-to-face interactions that are irreplaceable by technology-mediated communication [46]. In the space-time contexts of these interactions in the organizational workplace, it would be advantageous for teams to have smaller physical distances-the 'spatial distance, average weighted degree'among team members.

5. Limitations and conclusion

A key limitation is that this was a cross-sectional study meaning that while I could identify novel correlations between *network collective intelligence* and spatial layout, and prestige, I could not ascribe causality or identify causal mechanisms for these correlations. Future studies could build on my findings by using longitudinal data to examine dynamics of *network collective intelligence* and physical space, and the temporal relationships between these two factors and organizational outcomes such as prestige.

This study examined the individual- and group-level effects of network collective intelligence and physical space on prestige. Network position and physical space have significant correlations with the number of prestigious projects an individual is a member of, contingent on the association between social networks and physical space. Furthermore, network structure and physical space are correlated with the perceived prestige and innovativeness of a project team. These findings on network collective intelligence and physical space contribute to the understanding of individual- and team-level correlations between social networks and organizational outcomes in physical space. Future studies could extend this work by incorporating longitudinal locational data that allow for causal linkages from movement in physical space by individuals to the face-to-face encounters and interactions that are essential to the formation and maintenance of social ties. The increased availability of location-tracking technology has significantly decreased the costs of collecting these types of data, making the collection and analysis of location data a fitting way to extend the findings in this study.

Data accessibility. Datasets and code are provided as the electronic supplementary material.

Competing interests. I declare I have no competing interests.

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Split between two worlds: automated sensing reveals links between aboveand belowground social networks in a free-living mammal

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Many animals socialize in two or more major ecological contexts. In nature, these contexts often involve one situation in which space is more constrained (e.g. shared refuges, sleeping cliffs, nests, dens or burrows) and another situation in which animal movements are relatively free (e.g. in open spaces lacking architectural constraints). Although it is widely recognized that an individual's characteristics may shape its social life, the extent to which architecture constrains social decisions within and between habitats remains poorly understood. Here we developed a novel, automated-monitoring system to study the effects of personality, life-history stage and sex on the social network structure of a facultatively social mammal, the California ground squirrel (Otospermophilus beecheyi) in two distinct contexts: aboveground where space is relatively open and belowground where it is relatively constrained by burrow architecture. Aboveground networks reflected affiliative social interactions whereas belowground networks reflected burrow associations. Network structure in one context (belowground), along with preferential juvenile-adult associations, predicted structure in a second context (aboveground). Network positions of individuals were generally consistent across years (within contexts) and between ecological contexts (within years), suggesting that individual personalities and behavioural syndromes, respectively, contribute to the social network structure of these free-living mammals. Direct ties (strength) tended to be stronger in belowground networks whereas more indirect paths (betweenness centrality) flowed through individuals in aboveground networks. Belowground, females fostered significantly more indirect paths than did males. Our findings have important potential implications for disease and information transmission, offering new insights into the multiple factors contributing to social structures across ecological contexts.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

Behavioural ecologists have long understood that social decisions have important fitness consequences for individuals, shaping key processes including foraging decisions, information flow, disease transmission and reproduction [1]. It has become increasingly clear that who-meets-whom within animal societies is rarely random [2] and that social structure is often produced by individual variation in social preferences within groups [3,4]. Social network theory offers useful tools for quantifying and understanding how this variation contributes to social structure [5–7]. This framework formalizes the classical view that repeated pairwise interactions give rise to social relationships that in turn contribute to emergent social structures [8]. Importantly, network analysis extends traditional approaches by offering well-defined, standardized metrics for characterizing the effect of an individual's characteristics on *direct* and *indirect* social connections [9–11]. Network metrics are, therefore, offering new insights into the ways that individual characteristics (e.g. life-history stage, sex), preferential relationships (e.g. coalition partners) and the presence of key individuals shape group stability and structure [3,12–18].

A parallel, but largely distinct, literature has emerged showing that many animals exhibit 'personalities' [19], defined as consistent individual differences in behaviour; e.g. in aggressiveness, boldness or sociability. Only a handful of studies have explicitly linked personality traits to animal social networks [20–24]. A closely related literature examines behavioural syndromes, defined as consistent and/or correlated behaviour across two or more situations [19,25,26]. In nature, the two situations for animals often involve one situation where space is more constrained (e.g. shared use of refuges, sleeping cliffs, nests, or burrows) and another situation in which movements are relatively free (e.g. in open spaces lacking architectural constraints). The latter may, therefore, permit a richer range of social behaviours and interactions.

Interestingly, although most animals live in two or more distinct habitats or major situations, most social network studies are limited to a single context or rely upon combined data without explicit considerations of ecological context [27]. Thus, despite definitive evidence that individuals in different situations often differ in their patterns of space use [28,29] and sociality [30], and this notion being discussed extensively in review articles [7,10,31], very few empirical studies explicitly examine links between social networks derived from different situations [27]. This is unfortunate because connectivity may contribute to important processes such as disease and information transfer [32-34]. For example, understanding whether networks are more connected in one habitat than the other may offer insights into contexts as a 'hot spot' of transmission [35-37]. Moreover, partitioning the differences in social network metrics between contexts for individuals of different life-history stages and sexes will likely provide insights into how social roles (e.g. for juveniles versus adults [3,38]) vary or remain consistent across situations. Thus, although data collected using different sampling methods are inherently challenging to compare [39], efforts to assess the effects of life-history stage and sex on *context-specific* social metrics for individuals should provide an enhanced understanding of mechanisms contributing to social structure [2].

Within a social network framework, three major, nonmutually-exclusive mechanisms may generate social structure: 'movement rules', 'social interaction rules' and 'individual characteristics' [3,6,40]. First, movement rules refer to the ways that daily patterns of travel to and from limited resources, such as a shared refuge or a clumped food source, can produce repeated spatial associations even in the absence of social preference [41]. For individuals that travel away from refuges each day to search for food, movement rules predict that animals sharing similar refuges will be most likely to socialize due to increased encounter rates. Second, social interaction rules describe the extent to which social partner choice drives social structure [6]. These rules emphasize factors such as homophily [42], the tendency for similar individuals (e.g. same life-history stage, same sex) to preferentially interact. For example, homophily occurs among juveniles during play [43,44] or among adult females with enduring social bonds [45]. Finally, individual characteristics, such as personality, life-history stage or sex of an individual may predict social network metrics within a context [3,31,38]. An individual's network position may also remain consistent across contexts, indicating a behavioural syndrome, or vary between contexts if individuals engage in context-specific social roles.

Here we studied a semi-fossorial mammal, the California ground squirrel, Otospermophilus beecheyi, to gain insights into the factors contributing to social network structures of freeliving mammals who split their lives between two major contexts: above- and belowground. This is important because very few studies simultaneously seek to explain the ecological aspects of above- and belowground behaviours in semi-fossorial mammals; for notable exceptions, see [46,47]. California ground squirrels are facultatively social rodents that offer an interesting mammalian system for elucidating the extent to which movement rules, social interaction rules, and/or individual characteristics (e.g. personality, behavioural syndromes, life stage, sex) predict social structure. Individuals reside at distinct geographical sites, called colonies, at which group members regularly socialize, forage and collectively mob predators aboveground, but also seek refuge belowground in communal burrow systems for protection from predation and harsh weather [48-50].

Our current study capitalized upon the natural history of these animals to examine the mechanisms promoting social structure in two distinct contexts: above- and belowground. First, movement rules predict that because burrows are refuges limited in their size capacity as well as in their spatial distribution and abundance across the landscape, individuals that share burrows may also socialize to the greatest extent aboveground due to their increased tendency to interact as they travel to and from the same location (burrow) each day to forage aboveground. Specifically, if movements away from refuges spatially constrain opportunities for aboveground social exchanges, then social network structure in one context (belowground) should predict that in a second context (aboveground). Second, social interaction rules predict that if individuals exhibit social preferences based on homophily, then they should associate most often with others of the same stage and sex. Finally, we investigated how individual characteristics shape direct and indirect social connectivity within above- and belowground social networks. If networks reflect animal personalities and/or behavioural syndromes, then the relative network positions of individuals should be consistent over time (between years) and between contexts (aboveground versus belowground), respectively [31,51]. Beyond the effects of individual identity, we also predicted that juveniles of both sexes and adult females should be the most connected within their social networks. Although surprisingly little is known about kinship and dispersal patterns for the California ground squirrel [50], groups are likely matrilineal (female-based kin structure) with male-biased dispersal, as seen across the ground squirrel lineage [52]. If this is the case, then adult females and their immature offspring should promote connectivity, as seen in other matrilineal mammals [3,53,54].



Figure 1. Novel automated-tracking system. (*a*) Live trapping and release of free-living California ground squirrels allow researchers to provide each individual with a unique fur mark for visual identification during social observations, ear tag for identification during trapping and passive integrated transponder (PIT) tag beneath the skin for detection by the monitoring system. (*b*) Movements are detected by scanning an individual's PIT tag every time it passed through a secure antenna loop inside of a burrow opening. (*c*) Data logger (Biomark, Inc., Boise Idaho) records information about the time of day, squirrels' PIT tag ID and burrow location for each movement event. (Online version in colour.)

2. Material and methods

(a) Field site and study subjects

We studied free-living California ground squirrels at Briones Regional Park in Contra Costa County, California (37.9377014 N, 122.1388542 W). At this field site, at least some members of the population remain active aboveground all year [55]. Breeding largely occurs from mid-February to April, with females typically only producing a single litter per year [55]. Adult females rear young in burrows until offspring emerge as fully weaned young (age: 45–60 days), after which young of the year spend the remainder of their first year as juveniles (61–364 days) before maturing into reproductive adults (older than 364 days) [55,56]. We focused on juveniles and adults in the current study because these individuals are regularly observed socializing aboveground and, thus, have ample opportunities to visit burrows belowground and to affiliate with colony members aboveground.

The precise connectivity of California ground squirrel burrow complexes is largely unknown [50]. Although most burrows are presumed of to lack connections, excavations show that some are comprised of interconnected tunnels with multiple openings (e.g. 6–20 openings) at the surface [55]. Most tunnels are 4.6 m long, but extreme cases report tunnels of up to 70 m [55,57]. Regardless of the precise interconnectivity or length of burrow systems, individuals that share any burrow opening on a given day have opportunities to socialize, share space and exchange parasites [58].

(b) Live trapping of free-living individuals

The current study was part of a long-term study at our main colony site (Crow). Since 2013, we have live-trapped, marked and released California ground squirrels using squirrel traps (Tomahawk Live-Trap Company, Hazelhurst, Wisconsin, USA) baited with black oil sunflower seeds and peanut butter at and around burrow entrances. This is primarily done during the summer months, from late May to early August (figure 1*a*). Traps were covered with pieces of cardboard for shade and checked at intervals of \leq 30 min. While safely contained in a cone-shaped, cloth handling bag [59], we noted the individual's weight, sex, anogenital distance and reproductive status and then released each individual at its site of capture. We used this information to assign the life-history stage and sex to each individual for each year of the study.

Upon first capture, individuals were given three types of identification (figure 1). First, a Monel metal ear tag (National Band and Tag Co., Newport, Kentucky, USA) was attached to one pinna for permanent identification. Second, a unique Nyanzol cattle dye mark (Greenville colorants: New Jersey) was applied to the back for visual identification during social observations. Third, we inserted a unique passive integrated transponder (PIT) tag (Biomark, Inc., Boise Idaho) beneath the skin as a reliable 'lifetime' barcode [60]. In 2016 and 2017, respectively, we live-trapped and monitored a total of 131 and 158 marked individuals across the entire colony site.

(c) Automated sensing of belowground activity

Automated tracking offers exciting opportunities for the study of animal social networks [61]. Because the social lives of subterranean animals are largely hidden from researchers due to the small size of the openings to belowground refuges [62,63], we developed a new method for monitoring belowground activity of burrowing animals reliant upon radio-frequency identification to detect small (less than 1 g) and inexpensive PIT tags. We stored information from each burrow complex on an external data logger powered by a single 6 V rechargeable battery (Model DC224-6 AGM, Full River Battery, USA). A single battery powered each system for two weeks. This approach offers advantages over other reality-mining approaches because of its low cost, extended battery life and low disturbance to subjects [61].

Starting April 2016, we deployed data loggers (Biomark, Inc., Boise Idaho, figure 1a-c) at two distinct data monitoring stations within the colony site. The first station covered activity over an area of 15.0. \times 14.8 m² ('Logs' area), whereas the second station covered an area of $17.8\times7.7\ m^2$ ('580' area). The two areas were separated by 86 m and squirrels were regularly observed travelling aboveground between them. A total of 12 antennae loops were attached to each data logger at each station. Each loop was placed at an active burrow entrance and detected movements by scanning the unique PIT tags of visitors (figure 1b). We validated that each loop accurately detected PIT tags by scanning tags in and out of loops and confirming that their time-date stamps were accurately stored on the SD card at each station. These 12 loops provided substantial coverage of active openings, covering roughly 90% of active burrow entrances at each burrow complex. We secured each antennae loop at a single burrow entrance with $10 \text{ cm} \times 2.5 \text{ cm}$ Fabric & Garden Staples (Easy Gardener Products, Inc., Waco, TX). Staples were placed into the dirt using a mallet without damaging the burrow architecture, obstructing the ability for the antenna to effectively read the PIT tag, or jeopardizing animal safety as squirrels passed through the antenna (figure 1b).

The data logger recorded the specific time, date and unique PIT tag number each time a tagged individual passed in or out of an antenna's loop (figure 1c). Each data logger and battery were hidden under their own $24^{\prime\prime}\times12^{\prime\prime}\times13^{\prime\prime}$ artificial rocks (Orbit granite valve box cover, Model # 53016) to protect equipment from weather and other disturbances. Squirrels adjusted quickly to the equipment; we detected the first squirrel entering a loop within 20 min. of deploying it. The automated-sensing system remains on-site and currently records data year-round. Loops are monitored weekly and reinforced with additional staples or repaired with electrical tape as needed. On rare occasions, we moved antennae from previously active burrows to newly active ones to ensure continuous coverage of most burrows; most changes occurred outside of our summer sampling periods, such as after a winter rainstorm or juveniles emerged at the start of the summer.

(d) Behavioural observations at field site

Social observations were conducted from 27 May to 27 July in two separate years: 2016 and 2017. Whereas the field site experienced a severe drought in 2016, rainfall returned to typical regional levels in 2017 (http://cdec.water.ca.gov/index.html). Most juveniles and adults of the year were marked during these entire periods and, thus, were easily observed during social observations and detected by the data loggers. We recognized animals aboveground in daylight within open grasslands by the unique fur marks we gave them. Animals were also detected belowground by their unique PIT tags at the two focal burrow complexes with consistently high antennae coverage.

The diurnal lifestyles of these animals make them particularly straightforward to observe aboveground [48,50]. Trained observers monitored the study colony primarily in the mornings (0800 to 1200 h) and some afternoons (1200 to 1400 h); most affiliative exchanges occurred between 0900 and 1100 h. Observers sat at a distance (\geq 20 m) to avoid influencing behaviour. Observers monitored multiple areas within the study colony each observation day of this study; at least two groups of observers simultaneously collected social data from each of the two areas being monitored belowground. Thus, these data provided excellent knowledge of affiliative interactions for animals observed at, between, or surrounding the two belowground monitoring stations.

We recorded all occurrences [64] of affiliative behaviours (socio-positive interactions) including greetings, proximity maintenance, social foraging and playing (for details, see ethogram [48,50]) using 10×14 binoculars (Eagle Optics Ranger Extra-Low Dispersion Middleton, WI). Briefly, greetings involved two individuals meeting head-on and touching noses, one individual rubbing its cheek on that of another squirrel, or one individual approaching a second head-on and rubbing its nose near the corner of the receiver's mouth [48,50]. Proximity maintenance occurred when one individual approached a second and sat in direct body contact or within less than 1 m of the second individual [50]. Individuals foraged socially when they consumed seeds, grass or other forage within less than 1 m [50]. Each unique play bout started with one individual initiating play slapping, boxing, chasing, mounting, pouncing or wrestling with a second individual and ended when one of the two individuals moved apart from the other [50].

(e) Above- and belowground social network parameters Networks are comprised of individuals (nodes) connected to each other (by 'ties' or 'edges'). In this study, nodes represented individual squirrels and ties represented weighted, symmetric connections between them. We selected colony-year as the unit of analysis to account for annual changes in colony composition attributed to births, deaths and dispersal [65]. We therefore constructed a total of four separate networks—one belowground network and one aboveground network for each year.

Ties within a network reflected the proportion of days each pair, A and B, were detected at the same burrow reader (belowground) or exchanged affiliative behaviours (aboveground). We elected to use the same sampling period (day) for both contexts to minimize differences in network construction. Day was used as the sampling period for two reasons. First, although recording the precise amount of time pairs of semi-fossorial rodents are simultaneously aboveground is challenging, measures of daily rates of behaviour offer robust measures of affiliation [65]. Second, because the precise connectivity of burrow entrances and exits is unknown, this measure captures daily overlap within a burrow opening regardless of whether pairs shared the burrow at the same time for a given day. We calculated simple association indices to measure the daily rates of pairwise associations in each context [2,66]. This index was appropriate for our study because all subjects in the current study were equally likely to be detected in both contexts [2,66].

Belowground associations were calculated as: (the number of days A and B were detected using the same burrow)/ (the number of days A and/or B were detected at one or more burrows). Aboveground associations were also calculated as: (the number of days A and B exchanged affiliative interactions)/(the number of days A and/or B were observed engaging in at least one affiliative interaction). Because even weak associations are potentially important for the maintenance of social structure, we analysed weighted, unfiltered networks based on all associations [67]. However, an individual had to be logged (via its PIT tag) at least once and observed engaging in at least one affiliative interaction aboveground to be included in the final aboveground and belowground networks for a given year. This was done to avoid spurious correlations between empty cells and to ensure that each pair had the opportunity to associate in both contexts [68].

We constructed each of the four networks using the package 'igraph' [69]. For each network, we calculated two different nodebased metrics. First, we calculated the 'strength', the weighted equivalent to degree in binary networks, as the sum of its association indices with all colony-mates divided by the number of other potential actors (minus the focal individual) [70]. This standardized metric corrects for the number of nodes in the network to measure the extent to which each individual node *directly* associates with all potential actors in the network. Second, we calculated 'betweenness centrality', defined as a count of the

number of shortest paths through a node. This *indirect* metric reflects how important a node is for connecting disparate parts of the network, offering insights into the roles that key individuals may play in the spread of disease or information transmission across networks [6,31,32]. Because investigating the distributions of metrics (e.g. degree distribution for binary networks) is the preferred method for comparing node-based metrics between networks [2], we plotted cumulative distributions for metrics derived from above- and belowground networks to describe their relative properties.

(f) Statistical analyses

All statistical tests were conducted in R v. 3.4.1 [71]. To account for the non-independence in our data, we implemented permutation tests when using relational data (dyads within social networks) to test hypotheses [67,72] and included random effects in generalized linear mixed effects models (GLMMs) to account for repeated measures [3].

First, to test the predictions of movement and social interaction rules, we implemented multiple regression quadradic assignment procedures (MRQAPs) to assess the extent to which belowground network structure (predicted by movement constraints) and/or trait similarity (predicted by the social interaction rule of homophily) predicted aboveground network structure. This regression framework was superior to the univariate quadratic assignment procedure (QAP) because it allowed us to simultaneously test for the effects of multiple predictor matrices on the aboveground affiliative association matrix. For each year, we constructed a model in which we regressed three predictor matrices: (i) belowground association matrix, (ii) stage similarity (juvenile-juvenile = 1, juvenile-adult = 0, adult-adult = 1),(iii) sex similarity (male-male = 1, female-male = 0, femalefemale = 1) on the response matrix: aboveground affiliative associations. Permutation tests used the 'double-semi-partialing' method [73] developed in the mrqap.dsp function from the R package 'asnipe', each with 10 000 permutations [74]. We deemed *P*-values of less than 0.05 to be statistically significant.

Second, we tested for the effects of individual characteristics. To examine the potential for individual consistency in network position across contexts and years, we implemented consistency tests designed to compare the ranks of node-based metrics derived from different networks [51]. We therefore compared ranked values for a single metric (e.g. strength, betweenness) for each test [51]. First, to examine the effects of individual identity across contexts, we conducted a single test for individual consistency of each node-based metric (strength or betweenness) between ecological contexts (above- or belowground network) within a year. Second, we evaluated individual consistency across time by comparing each node-based metric (strength or betweenness) within an ecological context (above- or belowground network) provide the two years of study.

We also tested whether the fixed effects of an individual's lifehistory stage and sex were significantly associated with the node-based metrics (strength or betweenness) within each ecological context using randomized network permutations. To account for the non-independence of relational data, we permuted the nodes (individuals) of networks (while holding the edges constant) to create a set of 10 000 randomized networks for each year within each ecological context [72,75]. We then calculated the node-based metrics based on each of the four sets of permuted data. From the observed data, we constructed separate models to explain the following predictor variables: (i) strength belowground, (ii) strength aboveground, (iii) betweenness belowground and (iv) betweenness aboveground. That is, we calculated the estimates (slopes) for the fixed effects of stage and sex on each context-specific node-based metric using GLMMs in lme4 [76] with a restricted maximum likelihood method, Gaussian

proximity maintenance ($N = 5555$ events)
a) sitting $<1 \text{ m}$ (N = 3373)
b) collective foraging ($N = 1727$)
c) sitting in body contact ($N = 326$)
d) following ($N = 129$)
greetings ($N = 1228$ events)
a) nose to nose (N $=$ 720)
b) nose to cheek ($N = 508$)
play ($N = 1967$ events)
a) play wrestle ($N = 952$)
b) play pounce ($N = 384$)
c) play chase ($N = 234$)
d) play slap ($N = 227$)
e) play mount ($N=$ 85)
f) play grab ($N = 45$)
g) play push (N = 28)
h) play bite ($N = 12$)
allogrooming ($N = 4$ events)
*Exchanges involved juveniles (2016: $N_{\rm F}=$ 36, $N_{\rm M}=$ 26; 2017:
$N_{\rm F} =$ 36, $N_{\rm M} =$ 27) and/or adults (2016: $N_{\rm F} =$ 28, $N_{\rm M} =$ 11;
2017: $N_{\rm F} = 35$, $N_{\rm M} = 21$).

distributions and the random effects of identity and year for the observed data. We also extracted 10 000 model estimates from GLMMs run on the 10 000 permuted values of the fixed effects of stage or sex on each metric within an ecological context. We tested the statistical significance of the effects of stage and sex for each model by comparing the parameter estimates from the observed data to randomizations of each dependent variable. In electronic supplementary material, S1, we compared the estimates from our observed dataset (blue lines) to the distribution of randomly generated estimates and considered those effects falling outside of the 95% confidence interval (within the areas with red bars at the tails of each distribution) to be statistically significant.

3. Results

From 27 May to 27 July, we monitored a total of 101 (2016) and 119 (2017) individuals aboveground during social observations and 98 (2016) and 89 (2017) individuals belowground. Aboveground, we recorded a total of 10975 affiliative social interactions over 297 observation hours (2016: N = 5662; 2017: N = 5313 affiliative interactions). Of these, both identities were known for 8754 affiliative interactions (table 1). We also collected 17726 recordings of individuals moving in or out of burrows. On average, each loop detected 2.0 ± 0.3 (2016) and 2.3 ± 0.1 (2017) unique squirrel visitors per day (range: 0 to 16 squirrels per loop per day). We detected belowground movements for juveniles (2016: $N_{\rm F} = 28$, $N_{\rm M} = 28$; 2017: $N_{\rm F} = 22$, $N_{\rm M} = 15$) and adults (2016: $N_{\rm F} = 29$, $N_{\rm M} = 13$; 2017: $N_{\rm F} = 35$, $N_{\rm M} = 17$). In 2016 and 2017, only 16% (N = 16) and 18% (N = 16) of these individuals, respectively, were detected at both monitoring stations within the same summer; this suggests that a small proportion of individuals bridged connections in belowground networks.



Figure 2. Below- and aboveground social networks. (*a,b*) Belowground networks: blue ties reflect shared daily burrow associations. (*c,d*) Aboveground networks: red ties reflect daily exchanges of affiliative behaviours. To enhance the visibility of network features, node positions within networks were placed using the Fruchterman–Reingold algorithm (igraph R package [69]). For all networks, tie thickness is proportional to the simple association index (Al). For visualization purposes only, networks are shown as filtered networks (Als > 0.08). Individual attributes are reflected by node shape (circle: juveniles; square: adult) and colour (turquoise: male; green: female). The 2016 network contained 37 juveniles (number of females (N_F) = 20, number of males (N_M) = 17) and 23 adults (N_F = 19, N_M = 4) and the 2017 network contained 29 juveniles (N_F = 18, N_M = 11) and 32 adults: N_F = 22, N_M = 10). Letters represent abbreviations that correspond to fur marks for each individual squirrel (capital letters: in networks for both years; lower-case letters: in networks for a single year). (Online version in colour.)

(a) Distributions of node-based metrics in two ecological contexts

Overall, the *direct* metric of network connections (strength) was generally higher for nodes within below- (figure 2a,b) than aboveground networks (figure 2c,d), a pattern reflected

by comparing the cumulative distributions of strength for each network (figure 3*a*). In 2016, strength belowground was roughly twice as high (mean \pm s.e.: 0.039 \pm 0.004, range: 0.00 to 0.137) as aboveground (0.020 \pm 0.002, range: 0.00 to 0.060, N = 60 individuals). In 2017, strength was roughly four times higher below- (0.063 \pm 0.006, range:



Figure 3. Cumulative distribution of node-level network measures. (*a*) Standardized strength: average level of association for each node, a weighted measure equivalent to node degree in binary networks. (*b*) Betweenness centrality: number of unique path lengths that flow through each individual node. Measurements are plotted for spatial and social networks in 2016 and 2017. (Online version in colour.)

0.000 to 0.187) than aboveground (0.016 ± 0.001 , range: 0.000 to 0.047, N = 61 individuals). By contrast, the *indirect* metric (betweenness), defined as the number of shortest paths that pass through an individual, was consistently higher for aboveground networks (2016: 67 ± 11 paths, range: 0 to 378 paths; 2017: 79 ± 15 paths, range: 0 to 517 paths, figure 2c,d) than for belowground networks (2016: 35 ± 8 paths, range: 0 to 284; 2017: 33 ± 5 paths, range: 0–174 paths, figure 2a,b). The cumulative distributions reflect these patterns (figure 3b).

(b) Belowground networks, but not homophily, predict aboveground social networks

For both years, the full models including all three predictor matrices (belowground associations, stage similarity and sex similarity) captured a statistically significant amount of variation contributing to aboveground affiliative networks (MRQAP: 2016: $F_{3,1766} = 58.37$, p < 0.0001; 2017: $F_{3,1825} = 55.78$, p < 0.0001). Despite their statistical significance and, thus, statistical support of our predictions, these models only captured a small portion of the variability of the aboveground networks (adjusted $R^2 = 0.089$ in 2016 and 0.082 in 2017).

As predicted by movement rules, the structure of belowground networks (figure 2a,b) was positively correlated with that of above ground affiliative networks (MRQAP: R = 0.228in 2016; R = 0.130 in 2017; p < 0.0001 for both years, figure 2c,d). That is, pairs that occupied burrows at the same location on the same days were significantly more likely to exchange affiliative behaviours aboveground than were pairs that rarely visited similar burrows. This finding is consistent with the notion of movement rules because individuals seeking safety at similar burrow complexes (home bases) were presumably also most likely to encounter each other aboveground as they moved towards or away from these refuges. Beyond these effects, stage similarity negatively predicted aboveground networks such that juvenileadult dyads tended to socialize most often aboveground (figure 2). These effects were statistically significant in 2016 (R = -0.008, p = 0.001) but not in 2017 (R = -0.003, p =0.184). Although consistent with the notion that social interaction rules matter, our finding that individuals tended to associate most often with individuals belonging to a lifehistory stage different from their own is in direct contrast to the prediction of homophily. Sex similarity, however, failed to predict aboveground networks (2016: R = -0.001, p = 0.807; 2017: R = -0.001, p = 0.836).

(c) Node-based metrics consistent for individuals between contexts

Within a year, an individual's strength in its social network was consistent between above- and belowground ecological contexts (consistency permutation tests: 2016: N = 60, p = 0.001; 2017: N = 61, p < 0.0001). This confirms that individuals highly connected belowground are also the most socially connected aboveground. Moreover, an individual's metric of betweenness within a year was generally consistent between above- and belowground contexts; betweenness was significantly consistent for individuals between contexts during the summer with typical rainfall (2017: N = 61, p = 0.031) but not in the summer during a drought year (2016: N = 60, p = 0.311).

(d) Node-based metrics only consistent between years belowground

To test for consistency between years, we applied consistency tests to data for the subset of individuals (N = 19) monitored in both years. Belowground, an individual's strength (p = 0.033) and betweenness (p = 0.033) were consistent between years. However, individuals were not statistically consistent across years in their aboveground strength (p = 0.073) or betweenness (p = 0.098).

(e) Females important in fostering indirect connectivity belowground

After accounting for variation attributed to the random effects of individual identity and year, life-history stage and sex had limited effects on node-based metrics (see electronic supplementary material, S1). Life-history stage failed to significantly predict either the *direct* metric of strength or *indirect* metric of betweenness above- or belowground (p > 0.05 for all comparisons with null models; for details, see

electronic supplementary material, S1). We also did not detect an effect of sex on strength in either context or on betweenness aboveground (p > 0.05, S1). However, sex had a statistically significant effect on betweenness belowground (p < 0.01, S1). That is, on average, roughly five times as many of the shortest paths between nodes passed through females (betweenness: 44+7 paths) as through males (9+4 paths; figure 2).

4. Discussion

(a) Social selectivity in networks across ecological contexts

Our study uncovers new linkages between belowground architecture and the patterns of aboveground sociality for subterranean mammals, suggesting that social interactions belowground indeed are correlated with (and likely constrain) those occurring aboveground. Consistent with movement constraints, belowground associations predicted aboveground affiliative networks, but social interaction rules were also important because we found preferential juvenile-adult associations (regardless of the sexes involved). These relationships persist despite the inherent challenges of comparing data collected using different methods. The unexplained variation between our networks might be attributed to methodological and/or ecological differences. Individual characteristics also contributed to social structure. Although the explanatory value of life-history stage and sex on social structure was generally low, females had the highest betweenness belowground, fostering more indirect connections than males. Beyond this, social metrics were generally consistent for individuals over time (suggesting personalities) and between two major ecological contexts (suggesting behavioural syndromes) [51,77]. Both of these final findings contradict the common simplifying assumption of random mixing within populations made by traditional game theoretical models [31].

(b) Movement rules and social partner choice influence

network structure

Although aboveground networks are relatively open and free compared to those occurring inside the confines of belowground tunnels, our finding of correlated network structures is consistent with the notion that movements away from burrows influence aboveground behaviours. Access to limited refuges is likely a major factor shaping movements, and thus, patterns of social behaviour, as occurs in other species of mammals [14,78,79] as well as in birds [17,80], reptiles [40] and insects [81,82]. Ground squirrel burrows are limited refuges that offer protection from weather, safety from predators, and a place for hoarding food or rearing offspring [50,57,83]. Whereas social partners may simply interact most often with those they encounter near shared burrows, individuals may alternatively actively seek associations with the same partners aboveground independent of burrow preferences [84,85]. Distinguishing between these factors is important because models of social evolution, regardless of whether behaviours are favoured by direct or indirect fitness benefits, often require viscosity, defined as environmental restrictions on movements [4,86,87]. Empirical data such as ours are important because

game-theoretic models often make opposing predictions, predicting that spatial constraints may either promote [88,89] or inhibit [90] the emergence of socio-positive behaviours, both of which may be shaped by the animal's built environment [62,91].

Social interaction rules explained network structure. We documented preferential direct associations between juveniles and adults as well as the importance of *indirect* connectivity by females in belowground networks. These findings are consistent with the presumed matrilineal structure for this species [50] and what is known about other mammalian species living in matrilineal societies [18,92,93]. First, preferential aboveground connections between juveniles and adults suggest that parent-offspring bonds likely persist after weaning; pedigree information is required to confirm this and is not yet established for our subjects. Second, juvenile-adult preferential connections are also largely expected; juveniles often associate with adults to reduce predation risk [65] and sometimes initiate play with adults [43,44]. Finally, females likely reside at their natal burrows, fostering indirect links with other members of the social group. Kinship explains social network structures in many mammalian societies (e.g. [3,14,94-96]). Studying its effects on California ground squirrel networks should prove fruitful after a pedigree is established.

(c) Individual consistency in network position

Our finding that some individuals consistently occupied key positions in social networks across time (personalities) and major ecological contexts (behavioural syndromes) extends previous studies documenting consistent personality traits across time, seasons and/or behavioural categories [22,97]. These traits likely have fitness consequences for individuals [51] and may predict patterns of group-level behaviour [31], such as mobbing of predators [98] or policing of social conflicts [12]. Our results should inform our understanding of how connectivity by key individuals shapes the transmission of disease, information and genetic material within animal populations [51].

Despite our general finding of individual consistency in network metrics, betweenness was consistent between contexts in the summer with typical rainfall (2017), but not in the summer during a drought year (2016). Several other mammalian species [54,99,100] vary the strength of their direct associations in response to rainfall. Future studies spanning additional years should, therefore, conclusively elucidate whether ecological perturbations associated with drought disrupted otherwise consistent network positions in the California ground squirrel.

(d) Implications for understanding flow across dynamic networks

Our finding that individuals tend to occupy consistent network positions from one ecological context to another has important implications for understanding transmission networks. Within the context of disease, heterogeneity in contact rates may determine whether a disease dies out or becomes epidemic [36,101,102]. Parasites may be directly transmitted from one individual to the next (e.g. via direct social interactions) or transferred indirectly when potential hosts visit locations used earlier by infected hosts (e.g. via

space-use overlap [103]). This may produce time-lagged interactions [104]. Modelling pathways for parasite (disease) transmission in the ground squirrel system should prove particularly useful; these hosts may carry fleas and ticks that transmit zoonotic diseases (e.g. plague, Lyme disease, tularaemia and relapsing fever [50,105]). Flea density varies among burrows [58] and flea abundance on hosts varies with microhabitat use by hosts [106]. Study of individual differences in social personalities should thus offer additional insights into parasite transmission.

Applications of automated technologies are also revealing how social information spreads across animal groups [107]. For example, these technologies offer a rare glimpse into how social innovations spread across foragers [108]. Network structure also has implications for prey species, fostering the detection of and cooperative protection against predators [109]. Because California ground squirrels rely upon multiple modes of communication to locate food and cope with intense predation via the production of alarm calls [50], studies of communication networks may similarly explain the extent to which acoustic and/or olfactory information about food sources and predation risk flows across the social networks of ground squirrels.

(e) Conceptual framework for uncovering animal social networks

Our research establishes a novel approach for future studies aiming to understand how interactions in constrained spaces (that may or may not involve direct contact) and those occurring in relatively unconstrained spaces (e.g. aboveground, in the air, or in open aquatic environments) contribute to social structure. First, we offer a dependable, inexpensive alternative to heavier and more expensive proximity collars [47,110,111] and extend previous network studies that capture activity in other closed spaces, such as at nests and roosts [85,108,112], by capturing belowground activity. Second, we establish a conceptual framework for combining the use of two straightforward methods-direct social observations and passive data logging-to study networks in multiple contexts and across time. Automated measures should, therefore, complement insights gained from direct observations. Going forward, integration of both approaches should offer new insights into social structures for animals that socialize in easily observable, open spaces but that also visit relatively hidden architectural structures at fixed spatial locations for which direct observation is

prohibitive, such as occurs in fishes [113], birds [108,114], bats [85,95] and other semi-fossorial mammals [63,110]. Comparing networks should prove particularly useful for understanding how heterogeneities in node connectivity may affect disease [36,37,115] and information [116,117] transmission (flow) dynamics across contexts. Further investigations into the processes producing social structures and the role of key individuals across multiple habitats or major situations should, therefore, elucidate the ecological rules that generate and maintain social structures across animal societies more broadly.

Ethics. All field methods were approved by the Mills College Animal Care and Use Committee and were consistent with the guidelines of the American Society of Mammalogists for the use of wild mammals in research [118]. Research permits were obtained from the California Department of Fish and Wildlife and the East Bay Regional Park District.

Data accessibility. Data have been deposited in the Dryad repository [119]. Authors' contributions. J.E.S., D.A.G. and A.S. designed the field study. J.E.S., D.A.G., J.M.S., S.J.T., C.A.O. and R.D.H. contributed to data collection for this field study. J.E.S. carried out statistical analyses. All authors contributed to writing the manuscript and approved the final version for publication.

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12

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Exploring nest structures of acorn dwelling ants with X-ray microtomography and surface-based three-dimensional visibility graph analysis

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The physical spaces within which organisms live affect their biology and in many cases can be considered part of their extended phenotype. The nests of social insect societies have a fundamental impact on their ability to function as complex superorganisms. Ants in many species excavate elaborate subterranean nests, but others inhabit relatively small pre-formed cavities within rock crevices and hollow seeds. Temnothorax ants, which often nest within acorns, have become a model system for studying collective decision making. While these ants have demonstrated remarkable degrees of rationality and consistent precision with regard to their nest choices, never before has the fine scale internal architecture and spatial organization of their nests been investigated. We used X-ray microtomography to record high-resolution three-dimensional (3D) scans of Temnothorax colonies within their acorns. These data were then quantified using image segmentation and surfacebased 3D visibility graph analysis, a new computational methodology for analysing spatial structures. The visibility graph analysis method integrates knowledge from the field of architecture with the empirical study of animalbuilt structures, thus providing the first methodological cross-disciplinary synergy of these two research areas. We found a surprisingly high surface area and degree of spatial heterogeneity within the acorn nests. Specific regions, such as those associated with the locations of queens and brood, were significantly more conducive to connectivity than others. From an architect's point of view, spatial analysis research has never focused on all-surface 3D movement, as we describe within ant nests. Therefore, we believe our approach will provide new methods for understanding both human design and the comparative biology of habitat spaces.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

Visualizing the elaborate and dynamic architecture of social insect nests provides insight into how these societies function [1–4]. Driven by self-organization at the individual worker level, order emerges at the whole-colony level based on interactions between relatively uninformed workers following simple rules in the absence of a leadership hierarchy [5–8]. Examples of emergent order in social insect systems include the division of labour [9], adaptive shape of nest galleries [10,11] and quorum sensing to locate a new nest [12,13]. Architectural elements associated with nests can have impacts on the growth efficiency [14], physiology [15–17], immunity [18–21] and *per capita* productivity [22,23]. In order to study the collective decision making and building behaviours of these colonies, there are generally two options, each with its own strengths and weaknesses. One could examine nest building in a laboratory setting by creating

relatively simplified contexts [24–26]; however, this approach neglects the natural habitat and the environment. Alternatively, one could investigate the structure of natural nests; however, this method often requires the destruction of the colony [27–29]. To balance these aims, we investigated the nests of a social insect model system, the acorn-dwelling ants, using X-ray imaging and new analytical methods for studying architectural and social connectivity.

To better understand acorn-dwelling ant nest architecture, we applied computational methodologies commonly used in human architectural analysis. While there are a number of computational analysis methodologies used, one of the most important and widely used is visibility graph analysis (VGA) [30]. VGA analyses the properties of visibility fields by incorporating ideas from space syntax theory [31], early foundation work on visibility fields [32,33] and graph theory [34,35] with details of the visual experience of buildings and urban environments. The concept of the 'isovist' [32], which has had a long history in architecture, geography and mathematics, is central to visibility analysis. An isovist (figure 1) is 'the set of all points visible from a given point in space and with respect to the surrounding environment' [32]. Isovists are an intuitively useful way of thinking about a spatial environment because they provide a description of the space 'from inside', a point of view of agents as they perceive, interact and move through the environment [30].

Until recently, the majority of VGA research was conducted only on a single planar space and with a limited spatial complexity. A recent reformulation of VGA [36,38] incorporated multi-dimensional spatial properties and complex visuospatial relations to create a three-dimensional (3D) VGA analysis focused on human habitable spaces (figure 1). In this paper, we apply VGA methods to quantify and better understand the 3D structure and complexity of a social insect nest, the cavity occupied by acorn ants. Ants within these nests may not use vision, but the ray-casting method we developed is relevant to multiple sensory modalities including mechanical and chemo-sensory interactions.

2. Temnothorax X-ray imaging

The nests of many social insect societies can be extensive, housing millions of individuals along with their symbionts and parasites across networks of thousands of interconnected chambers [39]. However, in other cases, smaller colonies may occupy what appear to be much simpler spaces such as the hollow cavities of seeds [40]. As acorns decay and are parasitized, they become hosts to a complex ecosystem of microbial and invertebrate inhabitants, often including whole ant colonies [41]. Mary Talbot described the natural history of acorn ants, remarking on their abundance, their reliance on curculionid beetle larvae having eaten some portion of seed to make a cavity, and suitability for occupation depending on the condition of the acorn with respect to its decay and placement on the forest floor [42,43]. In a recent systematic survey of cavity-dwelling ant species in southeastern USA, the inspection of 6741 nuts from 68 trees revealed 36 species of ants within these cavities, the most common among them being Temnothorax curvispinosus [44]. Colonies, ranging in size from queens and a few workers to over 200 individuals, overwinter within the acorns [40,45-47]. Competition for nest sites is influenced by the size of the cavity and is believed



Figure 1. Spatial analysis and architectural computation. (*a*) Illustration of a traditional method of assessing connectivity, using an isovist to determine the set of all points/locations visible from a given vantage point in space and with respect to the center/starting location. In 3D visibility graph analysis [36], the isovist approach is carried out in three dimensions, comparing the connectedness between all points in space with each other, represented by the colour-coded array in (*b*). In (*c*), spatial relations of visibility and accessibility, which in traditional analysis presented challenges, are encoded into a mixed-directionality graph as a way to differentiate the intervisible lines of sight and potential walkable paths between two locations [37]. The surface-based graph analysis method we developed and applied in this study builds on the foundation from these earlier approaches to expand spatial analysis to new dimensions and contexts.

to shape community structure [48,49]. Consistent with the requirements of their life history, acorn ants have demonstrated consistent geometric preferences in cavity dimensions and

the ability to precisely discriminate between alternative nest geometries when given a choice [23,50]. These species also engage in complex house-hunting behaviour, using direct nest-mate contact rates to detect a quorum and make decisions in a remarkably rational manner [12,13,51]. Despite their near ubiquity in social insect research, relatively little is known about the architecture and spatial organization of *Temnothorax* within their natural nests.

We collected acorns resting in the forest leaf-litter near Providence College (Rhode Island, USA) that contained live acorn ant colonies (electronic supplementary material, video S1). To determine that the colony was alive without breaking the acorn open, we searched for worker ants (on average about 2-3 mm long) visible on the forest floor (e.g. foraging or scouting for a new nest). The worker ant was followed back to her nest. Having collected a number of these, we brought the acorns to Union College for X-ray imaging. X-ray imaging is a powerful tool to visualize structure and discover novel biological function in diverse systems ranging from the rhythmic pulsations of insect tracheal systems [52] to the four-dimensional morphology of large vertebrates in locomotion [53]. As a tool for non-destructive morphology, X-ray microtomography has helped to identify and classify a number of ant species, including some preserved within amber [54,55], as well as visualize the natural cavities inhabited by small insects [56,57]. Indeed X-ray imaging of artificial ant nest enclosures in the laboratory has been used to study social insect digging and building behaviours; however, using X-rays to examine these behaviours and the 3D spatial nest organization in natural conditions is technically challenging [28]. Acorn ant colonies should be model systems for this kind of investigation because they offer the advantages of being relatively small and desiccation-resistant, contained within natural cavities, and with low-tempo activity profiles.

Initially, we recorded tomography data using living acorn ant colonies. However, the ants moved in response to the X-ray energy, making image reconstruction impossible. Even the projection-X-ray video in real-time revealed only blurred images as the ants were far more active, due to the X-ray energy, than typically expected for these colonies. As a consequence, we were forced to flash freeze acorns in liquid nitrogen prior to subsequent imaging. The acorns were then warmed to room temperature, wrapped in parafilm, and mounted for scanning in a SkyScan 1272 (Bruker) micro-computed tomography (microCT) system. The acorns were scanned with the X-ray source voltage set to 50.0 kV and the X-ray source current of 200 µA. The best contrast was achieved using a 0.25 mm aluminium filter during the scans. Scans, length and resolution varied. One acorn was scanned for over 14 h at a pixel resolution of 6.08 µm with three X-ray image projections recorded every 0.05° through 180° of rotation. We also scanned two other acorns over 1 h with a pixel resolution of either 17.0 or 19.3 µm. In both cases, X-ray projections were recorded every 0.1 degrees through 180° of resolution. We found that this shorter scan time and resolution were sufficient to analyse the nest cavity architecture and identify the individual ants (figure 2).

The tomographic volumes were reconstructed from projection X-ray images using NRecon software (Bruker). Reconstructions made it possible to clearly visualize the structure of the nest cavity and positions of individual queens, workers and brood (figure 2 and electronic supplemental material, movies S1–S3). The reconstructed image stacks were analysed using CTan (Bruker) to segment the

hollow nest cavity and create 3D surface and volume models. Volume data were subsequently visualized using CTVox (Bruker), nest cavity surface areas and volumes were calculated and 3D shape files describing the nests were exported and used for the surface-based 3D VGA.

3. Surface-based visibility graph analysis

Before introducing the new methodology, we will review the underlying principles of the traditional planar VGA because our proposed approach could abstractly be viewed as a multi-dimensionally warped and convoluted re-imagination of two-dimensional (2D) VGA. The new methodology is internally extended through a multi-directional graph representation to work with Euclidean and non-Euclidean spaces [37,38]. In early experiments focusing on understanding spatial morphology, the volume of space visible from a location was simplified by taking a horizontal slice (2D) through the isovist polyhedron [32]. The resulting isovist is a single polygon (without holes) with calculable geometric properties such as area and perimeter. Through this process, the qualities of space, and their potential, are quantified and compared. When used for the analysis of landscapes, this method provided a 'viewshed' to '[take] away from the architectural space a permanent record of what would otherwise be dependent on either memory or upon an unwieldy number of annotated photographs.' [58]. In addition, similar ideas have been applied in the field of architecture and planning [59,60] and computer generated 'inter-visibility' topographic models [61]. A systematic analysis of isovists was performed by Benedikt [32], who believed that analysis of multiple isovists is required to quantify a spatial configuration and suggested that the way in which we experience and use space is related to the interplay of isovists.

Although Benedikt's methods were a leap forward [32], they were somewhat limited as spatial complexity increased. The main limitation is that isovists record only local properties of space, and the visual relationship between the current location and the spatial environment as a whole is not analysed. A second problem was that there was no systematic way to decode the results of the analyses, therefore, there was no framework that connects how isovists relate to spatial, aesthetic or morphological factors. Turner's VGA method combines earlier ideas of morphological analyses using graph theory with space syntax theory and small worlds analysis of networks to produce a graph of mutually visible locations in a spatial layout called 'visibility graph' [30,62,63]. The traditional VGA is implemented and widely used by both academics and practitioners through the open source 'depthmapX' spatial network analysis software [30,64]. A number of local and global graph-based measures of spatial properties [65] can be calculated in depthmapX. In space syntax, the measures can be extracted from the graph and compared with real-life data of usage to understand possible morphological or spatial correlations [66,67]. More importantly, the local graph measures can be used to understand and describe the shape and complexity of spaces [68].

(a) Two-dimensional and three-dimensional visibility graph analysis

Generating a 2D VGA is a two-step procedure. We first define a set of locations on the plan, which form the vertices of the visibility graph. Next, we employ ray-casting (visibility testing)



Figure 2. Visualizing acorn ant colonies with X-ray microtomography. In the first panel (*a*), three virtual cross-sections through acorns are shown, with lighter shades of grey associated with higher density plant and animal tissues. The centre image shows a cross section including a worker positioned near the nest entrance. The first and third images show a toroidal shape nest cavity surrounding seed tissue in the centre. Three-dimensional renderings of regions of interest within the scanned acorns are displayed in (b-e), illustrating the density of ants and the complexity of the cavity space within these nests. (*f*) A rendering from within one acorn's dataset showing a queen *T. curvispinosus* standing over a pile of her larvae. (*g*) A rendering of a relatively freshly fallen acorn that had not yet been parasitized or occupied by insects. (Online version in colour.)

techniques to construct the graph edges between vertices by expressing the direct visibility relations. The selection and construction of graph vertices is through a grid of locations covering a spatial system at regularly spaced intervals. In VGA, we select an appropriate grid resolution that adequately describes the spatial system with the goal to define a set of locations that offers a near-full description of the space. Moving to three dimensions, a simple 3D VGA analysis method [30] considers all spatial points as nodes in a graph. In particular scenarios, certain points cannot act as locations of activity or spatial importance because all-to-all 3D relations are inherently independent of natural occupancy; however, it can be helpful when investigating pure geometric or morphological relations. In this paper, we focus on a space that is dominated by complex chambers and spatial folds, where occupants can walk along all surfaces and with sensory detection potential for connectivity determined along the lines of the virtual ray-casting.

(b) Surface-based 3D VGA analysis

To take advantage of the complexity and level of detail that the 3D tomographic process captures, we developed a new

method to analyse the morphology of space from within the acorn. The reconstructed tomographic volumes were exported as shape files composed of a triangulated 3D mesh. The surface-based 3D visibility graph analysis (sbVGA) begins by subsampling the models to create a set of locations evenly distributed across all surfaces on the nest and to maintain the primary features of the space without excessive resolution that would add unnecessary computation time. As the average distance between subsampled coordinates was approximately 0.25 mm, a distance smaller than an individual ant, we are confident that by erring on the side of relatively abundant detail, nothing was missed in our analysis. For each mesh triangle, the centroid is considered as a possible location. This subset of centroids in space then acts as the graph vertices. A ray-casting connectivity check is executed between all pairs of vertices in the graph, establishing an edge if a direct connection exists between two locations in space. These connections and the subsequent 3D hollow 'isovist' represent a spatial graph structure describing the local morphology in a no-ceiling space. Spatial boundaries wrap around the location in question (because ants can move in any direction) and represent a new challenge for spatial analyses. The sbVGA graph is then analysed and selected graph measures are evaluated.

We quantified nest connectivity (or graph degree), closeness centrality (or integration) and local clustering coefficient following Hillier & Hanson's earlier work [31]. The connectivity of a location is equivalent to the degree of the vertex, as discussed in graph theory, and represents the number of connections (directly visible locations) that the node has with other nodes in space. Closeness centrality, or integration in classic space syntax literature, is directly linked with 'mean shortest path' from a location to all other locations in the system [30]. Closeness centrality is defined as 1.0 over the sum of all shortest paths between the location in question and all other nodes. This gives a statistically similar result to Hillier and Hanson's 'integration'. Mean shortest path is a representation that quantifies the accessibility of every location in a spatial system. If a location in the nest is on average harder to access through edges on the sbVGA graph then its mean shortest path value (or mean depth) will be high. Because mean shortest path or thus closeness centrality measures configuration by considering all locations with respect to each other in the system, global relationships between locations in the system can be explored. By contrast, connectivity and local clustering coefficient is a 'local measure' as it only accounts for the immediate accessible location. Clustering coefficient is defined as the number of connections between all the locations in the neighbourhood of the generating location in question, that is, the number of lines of sight between all the locations forming the isovist, divided by the total number of possible visibility connections with that neighbourhood size [30,62]. In 2D isovist terms this is equivalent to finding the mean area of intersection between the generating isovist and all the isovists visible from it, as a proportion of the area of the generating isovist. In our case, the sbVGA gives us a volume consisting of the structural and walkable walls of the nest from each location. Therefore, the measure relates to the convexity of the 3D volumes, or 3D hollow isovists, at the generating location because sbVGA only considers boundary location and not the empty middle space. If the 3D boundary isovist being considered is a convex volume, then almost all of the point locations within the neighbourhood will be able to see each other and clustering coefficient will tend to 1.0.

On the other end of the spectrum, when many points are not visible from each other, meaning the space is very spiky (or maybe has a higher inertia as a volume), clustering coefficients tend towards 0. Clustering coefficient also 'indicates how much of an observer's visual field will be retained or lost as one moves away from that point' [30, p.110].

4. Results and discussion

Contrary to our prediction and conventional wisdom that acorn ants inhabit relatively hollow spherical cavities, we found that the nests more accurately resembled multiple spaces defined by convoluted and partitioned surfaces, highly compartmentalized architectural elements, and discrete zones of connectivity. The presence of seed remnants, frass, layers of botanical tissue and multiple topological surfaces contributed to the complexity of these nests. For cavities that measured at their greatest width 23.7 and 25.2 mm diameter spaces, the surface areas and volumes that we actually measured were 1762.5 and 770.9 mm³ for one acorn (nest-101) and 2003.0 and 1424.9 mm³ for a second (nest-103). These measurements average to a surface area to volume ratio of 1.85, a value approximately 460% greater than the ratio expected for simple hollow spherical-shaped nest cavities.

Both nests analysed with sbVGA had a closely matched number of graph vertices (node counts): nest-101 has 10825 analysed locations and nest-103 has 10952. In space syntax and sbVGA, the comparison of the 'local' measures that describe the immediate surrounding of a location versus a 'global' one like closeness centrality that depicts the morphological relation between the location in question and all other locations helps us understand and quantify the intelligibility of a location, its structural characteristics, and may even expose certain abnormalities [69]. Intelligibility of a space allows us to recognize the global spatial complexity of an arrangement of spaces (or a network of space) by only looking around local space. In highly intelligible environments, orientation and navigation are inherently easier. Intelligibility is a correlation between connectivity and closeness centrality. It indexes the degree to which the number of immediate connections of a location in sbVGA is a reliable guide to the importance of that location in the nest as a whole. A strong correlation, or 'high intelligibility', implies that the whole can be read from the parts. Two main factors are dominant in both nests: the small, compact size and the almost spherical structure with only internal excavations. These features are translated into the balanced scatterplots of connectivity versus closeness and clustering coefficient (figures 3 and 4).

The distribution of connectivity and closeness values in both nests shows, through the 3D scatterplots (figures 3 and 4), that while both have a clear inner and outer wall structure, with connectivity values associated with the outer wall as expected (based on the greater range available for ray-casting), nest-103 with its barrel shape generated two distinct peaks in the distributions. The convoluted nature of nest-101 restricts the values of both local and global measures on the bottom part of the nest in favour of the larger chambers at the top. In contrary, the main corridor-like structure in nest-103 boosts the closeness centrality values near the two entry points as movement potential through this 'shortcut' is likely.

The queen and brood pile in nest-101 sits in a very interesting location. While the closeness centrality, or mean depth


Figure 3. sbVGA of nest-101. Parts (a,b) show the surface points used in the analysis colour-coded by connectivity (graph vertex degree) separated by a 230° rotation. Parts (c,d) show the analysed surface points colour-coded by local clustering coefficient, separated by a 230° rotation. Asterisks indicate approximate locations of the queen and brood pile. Parts (e,f) plot connectivity, as a description of local properties of space, against closeness centrality and clustering coefficient.

of the area from all other locations, is generally in the middle of the spectrum (all values are normalized between 0.0 and 1.0), local properties of space described by the clustering coefficient depict two adjacent areas where one has a very high value while the other has an extremely low value. In essence, the queen can be relatively accessible to the rest of the nest and also potentially control the level of immediate accessibility very quickly. The area with the low clustering coefficient is one of the areas of the nest that can be seen as top-ranked in terms of convexity; it is part of the largest cavity in that nest,



Figure 4. sbVGA of nest-103. (*a,b*) The surface points used in the analysis colour-coded by connectivity (graph vertex degree) separated by a 230° rotation. (*c,d*) The analysed surface points colour-coded by local clustering coefficient, separated by a 230° rotation. Asterisks indicate approximate locations of the queen and brood pile. (*e,f*) Plot connectivity, as a description of local properties of space, against closeness centrality and clustering coefficient.

so 'openness' and 'control' can be associated with it. The adjacent small chamber has the highest clustering coefficient value and can be seen as the perfect hideout, quickly minimizing the distance needed to almost disconnect or hide from the rest of the nest. The distance to the queen's location in comparison to the main nest entrance is one of the longest in the graph, within the top 20% and consistent with a spatial segregation that, in analysis of human dwellings, may be associated with a sense of security.

The queen and brood in nest-103 are located at the bottom on the barrel-shaped internal structure, seemingly random, but a closer analysis of the depth from the entrance and the structural analysis of the three total excavated cavities inside the nest give the location a similar character to nest-101. The uniform barrel shape gives the lower part of the nest equivalent graph depth complexity in relation to the entrance at the top. More interesting is that nest-103 has two main internal excavations that are clearly used as 'through movement chambers' allowing inner nest shortcuts, while the queen is located on the opposite side of the nest and segregated from these shortcuts. Based on the local clustering coefficient, the location characteristics depict good local control and some small 'covered' cavities close to the location. Global accessibility to the nest, described by closeness centrality, is uniform because of the barrel structure of the nest.

To our knowledge, unbiased graph-based spatial analyses have never been applied to analyse non-human animal architecture before. The benefits of this approach are (i) the automated and unbiased quantification of configurational relationships with reference to accessibility and other sensory factors; (ii) the comparisons from location to location within a system and the ability to compare systems with different geometries; and (iii) the relationship of sbVGA measures to manifestations of spatial perception, like movement and space use. The unbiased nature of this approach, based on the uniformly distributed 3D grid used as a basis for modelling nodes and the connectivity calculations, distinguishes it from other network-based studies of social insect nest architecture in which nodes and edges within spaces must necessarily be manually identified and classified by the investigator. The major limitation of sbVGA as currently implemented is that the ray-casting connectivity check algorithm used to determine which nodes are connected by edges is not affected by how far apart two nodes may be in space, a factor that may have biological significance depending on the sensory modality for interaction by individuals at these positions. Another limitation concerns the time costs of generating the 3D nest models. We scanned three acorns with ant colonies and a fourth without a colony (see image data presented in figure 2), but only two were used for sbVGA due to constraints primarily associated with the segmentation of the X-ray image datasets.

Although it is not possible to generalize that the architectural features described here are typical for all acorns and other types of nest cavities (e.g. hickory nuts, galls, rock crevices), our work represents a proof of concept with respect to X-ray imaging possibilities, how these data can be quantified using new sbVGA methods, and the potential for future application to habitable spaces in complex structures and novel environments for both humans and animals. Future research that includes more replication, a greater diversity of nest structures and different null geometric models will help us to understand more about how the building and nest-choice behaviours of ants fit into a broader ecological context. For example, the suggestion that acorn ants cultivate and may prefer nests with complex architecture is at least supported by the behaviour observed in laboratory nests when Leptothorax tuberointerruptus workers use sieved sand grains to build partitioning walls around their queen and brood pile [24,25]. Previous studies have demonstrated consistent preferences of Temnothorax colonies for nests of certain sizes and proportions [50], but we are unaware of any studies that have subjected these ants to nest-choice experiments in which the nest topology varied while potentially holding surface area and/or volume constant. When exposed to potentially stressful stimuli including temperature and microbial growth, T. curvispinosus colonies relocated within their acorn, moving larvae toward warmer regions and avoiding microbial contaminants [18]. Since a recent study has demonstrated the successful use of CO₂ anaesthesia to temporarily freeze insects for repeated X-ray microtomographic imaging scans [70], their movements and organization behaviours could be visualized at high resolution and tracked within relatively natural nest environments. In addition, the ray-casting method applied here could be modified (e.g. constrained to different scales or types of surface) to match the appropriate sensory modalities and provide a theoretical foundation for understanding how the architecture of inhabited spaces affects the dynamics of human and animal social networks.

Ethics. Research using the invertebrate animals in this study adhered to local guidelines and appropriate ethical standards.

Data accessibility. Additional data uploaded as electronic supplementary material.

Authors' contributions. T.V., S.D.K. and J.S.W. conceived the paper. S.D.K., A.G.S. and J.S.W. acquired and analysed X-ray imaging data. T.V. is responsible for the visibility graph analysis. T.V. and J.S.W. wrote the final version of the paper with input from all authors.

Competing interests. We declare we have no competing interests.

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9

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The non-additive effects of body size on nest architecture in a polymorphic ant

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Like traditional organisms, eusocial insect societies express traits that are the target of natural selection. Variation at the colony level emerges from the combined attributes of thousands of workers and may yield characteristics not predicted from individual phenotypes. By manipulating the ratios of worker types, the basis of complex, colony-level traits can be reduced to the additive and non-additive interactions of their component parts. In this study, we investigated the independent and synergistic effects of body size on nest architecture in a seasonally polymorphic harvester ant, Veromessor pergandei. Using network analysis, we compared wax casts of nests, and found that mixed-size groups built longer nests, excavated more sand and produced greater architectural complexity than single-sized worker groups. The nests built by polymorphic groups were not only larger in absolute terms, but larger than expected based on the combined contributions of both size classes in isolation. In effect, the interactions of different worker types yielded a colony-level trait that was not predicted from the sum of its parts. In nature, V. pergandei colonies with fewer fathers produce smaller workers each summer, and produce more workers annually. Because body size is linked to multiple colony-level traits, our findings demonstrate how selection acting on one characteristic, like mating frequency, could also shape unrelated characteristics, like nest architecture.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

Social insect nests serve complex physiological functions [1,2], organize labour [3] and act as protective fortresses for the colonies living within. Each nest is an extension of the colony phenotype and represents the response of its many builders to the external environment. Although every species produces a distinctive architecture, individual nests vary considerably around a mean set of characteristics, and some variants may increase colony fitness. Among ground-nesting species, variation in nest architecture has been attributed to season [4], soil type [5], soil moisture gradients [6,7], the presence of food or brood [8] and changes in colony size [9]. Though less well understood, differences in worker attributes, like age, morphology, experience or genetic background also have profound effects on nest structure. For example, old *Pogonomyrmex badius* workers excavate larger nests than young workers [10], and physical differences in male and female workers control the frequency of tunnel bifurcations in some termite species [11]. Likewise, large *Solenopsis invicta* workers in isolation excavate less than workers from their colony's natural size distribution [12].

Across colony ontogeny and during each annual cycle, social insect colonies alternately invest in growth and reproduction. Worker age structure [13], body size [14,15] and labour allocation [13,16] have all been demonstrated to vary with these changes in colony investment. Therefore, in each season, the abundance and composition of the work force available to build a new nest are distinct. When distinct worker types are combined, their individual contributions to nest architecture may be additive or non-additive. For example, if small workers tend to build



Figure 1. Average worker body size is related to season and colony identity in *V. pergandei*. (*a*) Distribution of worker head widths for eight monogyne *V. pergandei* colonies, sampled in four periods across 1 year (N = 1690 workers, from Kwapich *et al.* [18]). Colony-level variation in body size is shown across four periods for (*b*) large colonies and (*c*) small colonies. Colonies are shown in the same order in each season. Each colour represents a unique colony. Colonies that maintained a larger forager population and produced more workers annually did so by reducing worker size between spring and summer. On average, large colonies also contained fewer patrilines (1–4 versus 4–9). (Online version in colour.)

chambers and large workers tend to build shafts, a colony's nest architecture might be predicted from the number of large and small workers present. Alternatively, various ratios of interacting workers may yield new structures or processes not predicted by the performance of any single worker type in isolation. Like other colony-level traits, the additive and nonadditive elements of nest architecture can be investigated by manipulating a colony's underlying worker composition while holding environmental factors constant.

Veromessor pergandei is a polymorphic seed harvesting ant of the Sonoran and Mojave deserts, and an ideal species for studying the interplay between worker variation and variation in nest architecture. Within colonies, large workers are more than two times the size of small workers, and the abundance and frequency of each body size varies considerably across populations [17], across seasons [14,15] (figure 1a) and with respect to colony identity (figure 1b,c) [18]. Body size does not predict the seed size that each individual collects, or the tendency of an individual to participate in nest excavation and foraging behaviour. Rather, changes in body size allow V. pergandei colonies to maintain a stable work force, despite seasonal variation in resource abundance [15,18]. The largest colonies maintain a large foraging force by dramatically reducing new worker body size following sexual reproduction. Colonies with a high degree of seasonal polymorphism also contain fewer patrilines than smaller colonies, with less variable size frequency distributions [18].

Though no published descriptions of a complete nest exist to our knowledge, several partial excavations have revealed the incredible scale of *V. pergandei* nest architecture. Nests of mature colonies are characterized by a wide, central shaft that slants downward at a 35° angle, and reaches an excess of 3 m in depth. Numerous horizontal chambers and ancillary shafts project from the main shaft, and lateral tunnels may connect as many as 10 satellite entrances or secondary nests [9,19]. Foragers initiate the excavation of new nests along foraging routes (CL Kwapich 2015–2017, personal observation), and like other members of the genus, nest relocation takes place year-round, especially following rains [15,19–21]. In effect, *V. pergandei* nests excavated in different seasons, by colonies that differ in worker number and pedigree may have unique architectures due to the underlying size distributions of their builders.

In this study, we measured the additive and non-additive effects of worker body size on nest architecture in *V. pergandei*. We compared nests made by combined and isolated size classes to determine (i) if nest structures scale to the average worker

body size in a group, (ii) if workers of different sizes are responsible for particular features of the architecture (chambers, branches, etc.) and (iii) if the nests created by each size class in isolation differ from those produced by the interactions of multiple worker size classes in combination.

2. Methods

We compared nests excavated by *V. pergandei* workers from three, artificial body-size frequency distributions. Ants were foragers, collected from 13 colonies located in Casa Grande, AZ, USA, in September and October of 2017. Although never studied explicitly in this species, we chose foragers for a number of reasons that support their role in the establishment of new nests: across ant species, foragers are associated with the initiation of new nests [22–24]; we observed that foraging activity ceased or was strongly reduced when wild *V. pergandei* colonies excavated new nests; in a study of forager allocation across the annual cycle, marked foragers represented a large proportion of the excavating force; new nests were initiated along foraging routes and foragers were the only individuals to travel a substantial distance from the nest on these routes [18].

In *V. pergandei*, total body length ranges from approximately 3.5 to 8.4 mm [17], and all worker size classes contribute to the remodelling of old nests and excavation of new ones [15]. Head width is a good predictor of body size and has been shown to be correlated with both mesosoma length (r = 0.96) and mandible length (r = 0.89) across *V. pergandei* populations [17]. In our focal population, worker head widths (measured across the full width of the eyes) ranged continuously from 0.50 to 1.90 mm and served as a proxy for body size within colonies. To maximize observable differences in nest excavation, we selected workers from the largest and smallest thirds of the size distribution. In a pilot study, a nest made by all size classes was also cast and has been included in electronic supplementary material, S1.

Foragers from 13 colonies were vacuumed directly from foraging trails using a modified DeWalt[®], 20 V Max shop vacuum. Workers and accompanying soil were kept overnight in 30 cm × 15 cm storage bins, offered a mixture of grass seed, nutritional agar and cotton-plugged test tubes containing water. Twentyfour hours after capture, workers were divided into three treatment groups containing 60 individuals each. The first treatment contained 60 workers from the smallest body-size class only (head widths 0.5-1.0 mm), the second treatment contained 60 workers from the largest size class only (head widths 1.4-1.9 mm) and the third treatment contained a mixed group of 30 small and 30 large workers. Workers were sorted by size using soft forceps and a two-dimensional wedge-micrometre printed on clear acetate; similar to that developed by Porter [25].



Figure 2. Example of networks and corresponding nest casts produced by 60 small (*a*), 60 large (*b*), and a mixed group of 30 large and 30 small workers (*c*) from a single colony, CG010. Diamonds represent nest entrances, circles represent branching points, stars represent chambers, and squares represent terminations. Network edges are not scaled to shaft length. (Online version in colour.)

Each group of 60 workers was introduced into a 191 bucket containing 23 kg of sand and 1.5 l of deionized water packed into place (37 cm deep and 29.5 cm in diameter). Silica pool filtration sand was selected because of its comparatively uniform particle size (Quikrete[®], 0.45–0.85 mm, 20–40 mesh). Sand was compacted so that nest structures could be built without collapsing, and so that chambers and tunnels would maintain their integrity when liquid wax was later introduced as a casting material.

To ensure that digging took place in the centre of each bucket, workers were released into a 10 × 10 cm clear plastic box with a 1.5 cm hole drilled in the centre. The box also contained a ball of wet cotton, a cube of nutritional agar and beetle larvae as a food source. Workers began excavating sand between 6 and 35 min after introduction, and were allowed to dig for 48 h at 26°C before each trial was terminated (n = 39 nests obtained from three different treatments for each of the 13 colonies). Each box was closely monitored for the appearance of dead workers. Dead workers were replaced with individuals from the same colony and size class as soon as they were noticed (fewer than 5 in any replicate). Short film clips were taken of mixed-size class participated in excavation.

After 48 h, boxes were removed. Excavated sand was collected from the floor of each box, then dried and weighed to determine the total amount of sand excavated. Paraffin wax was heated and poured into the entrance of each nest to make a cast of the excavated space. Wax was chosen as a casting material because of its ability to flow into even the smallest of the excavated spaces and create a complete record before cooling [26,27]. After the wax hardened, surrounding sand was removed to reveal the architecture of each nest. Nests were carefully exhumed in pieces, arranged on a flat surface and photographed with a scale. Digital photographs were imported into *ImageJ* (US National Institutes of Health, Bethesda, MD, USA) and measurements were taken by tracing the length of each shaft and chamber after calibrating a 0.50 cm scale.

(a) Description of nest features

Nests consisted of a single entrance connected to a central shaft. The central shaft often branched into ancillary shafts with varying branching degrees as well as developing chambers. The fate of incipient tunnels could not be determined, but projections from a shaft greater than 1 cm in length (approx. two body lengths) were scored as unique branches. Developing chambers were identified as broadened horizontal projections from a shaft without additional branching of their own, and frequently contained clusters of workers visible through the wax cast. Nest length was measured as the sum of all branch lengths and of all chamber lengths, whereby chamber length was measured as a straight line between the shaft from which it arose and the far wall opposite to the shaft.

Prior to nest casting, a shop vacuum was used to remove loose sand and to create a shallow conical pit around the entrance of each nest. This allowed liquid wax to pool as it flowed into the nest entrance, rather than spreading across the surface of the bucket. The wide, conical feature visible in photographs at the top of each nest cast is, therefore, an artefact of the casting procedure and not a structure built by the ants.

Accurate measurements of shaft diameters and/or chamber volume cannot be taken from the exterior of wax casts because each feature is surrounded by a thick sheath of sand mixed with wax. Detailed measurements can only be taken from the internal diameter of cross sections of these nest structures, where a sand-free ring of wax is clearly visible. We did not measure shaft diameter directly. For the purposes of this study, we focused on the overall number and distribution of nest features, as well as the amount of sand displaced by each nest and the total length excavated.

(b) Nest casts as directed networks

We studied architectural complexity across different experimental treatments by interpreting the structure of each excavated nest as a network [12,28]. We considered a nest as a connected graph, G(V; E), consisting of a set $V = \{1, ..., N\}$ of N vertices (or nodes) and a set $E = \{\langle i_1, j_1 \rangle, \dots, \langle i_k, j_k \rangle\}$ of *k* edges connecting a pair of nodes *i* and *j*. Nest entrance, branching points, chambers and shaft terminations represent different types of nodes of the network. Shafts represent edges of the network connecting a pair of nodes. A distinctive trait of V. pergandei nests is the absence of multiple shafts connecting the same pair of points (e.g. a branching point with a chamber) that would form a closed loop. Consequently, the nest architecture was well described by means of directed edges pointing downward from the entrance. The resulting network is, therefore, a directed acyclic tree. Additionally, edges were described by an attribute giving the length of the corresponding shaft. We numbered nodes following a breadth-first search strategy to traverse the resulting tree whereby the root of the tree (i.e. the nest entrance) was always node 1 and the last leaf of the tree (i.e. the right-most node) was node N. Figure 2 shows examples of the networks resulting from three different group compositions of workers and their corresponding nest casts.

(c) Body size and excavation

During excavation, *V. pergandei* workers transport boluses of sand between their mandibles and a psammaphore (basket of hairs) on the ventral side of the head. We measured the amount of sand carried per excavation bout across a full range of worker sizes. To do



Figure 3. Distributions of (*a*) nest length and (*b*) excavated sand weight by treatment. Colonies are denoted by points and their identity by colour. Nests excavated by a mixed group of 30 large and 30 small individuals were significantly longer than those built by 60 large or 60 small workers alone. Nests built by mixed groups were also significantly longer than expected based on estimates from each single-sized worker group (expected). Mixed groups excavated significantly more sand than expected based on the number of large and small workers present. (Online version in colour.)

so, foragers were collected from three field colonies in November of 2017. After 24 h, mixed-size groups of workers were placed in clear plastic boxes with a 1.5 cm hole in the centre. Each box was centred on top of a bucket containing 0.45-0.85 mm sand as detailed above. As workers departed with sand loads, they were collected using a mouth aspirator (n = 32). Each captured ant and the sand she carried were photographed on a gridded Petri dish. The number of collected sand grains was related to head width through linear regression, and an average number of grains collected per trip was calculated for those workers that belonged to the designated 'large' and 'small' size classes.

(d) Analysis of nest architecture

To determine if worker size influenced nest size, we compared nest length and sand weight excavated by three different worker size distributions. Owing to the normality of data, we used Linear Mixed Models (LMMs, R v. 3.4.0, package lme4). Nest length and sand weight represented our response variables, treatment was the fixed effect and colony identity was the random effect. Post hoc, pairwise comparisons between treatments were made with Tukey's HSD tests (R package *lsmeans*). Additionally, differences between expected nest size (length or sand weight) and the observed nest sizes of mixed groups of 30 small and 30 large workers were determined using similarly defined LMMs. For each colony, the expected nest size was estimated as the average nest length or weight of sand excavated by both single-sized worker groups from the same colony-in other words, 50% of the nest produced by the smallsize group added to 50% of that produced by the large-size worker group for each colony (n = 13 colonies).

The complexity of nest architecture can be described through network analysis [12,28]. The number of nodes and the number of edges provide a direct way to assess the size of a network. Although nodes and edges represent very different structures of a nest, their total numbers are correlated because in a directed acyclic tree the number of nodes equals the number of edges plus one. Therefore, we considered only the number of edges. Additionally, an ensemble of directed networks can also be characterized in terms of the in- and out-degree distributions, which give the probability of finding a node in the network with a certain number x > x0 of ingoing and outgoing edges. For the purposes of our study, we focused on the out-degree distribution only and ignored nodes without outgoing edges (i.e. x > 0) to characterize the number and type of branches in different nests. The effects of treatment on each of the components of complexity were assessed using a Generalized Linear Mixed Model (GLMM) with a logarithmic link function. Number of edges and branching factor represented our response variables with a Poisson distribution; treatment was the fixed effect, and colony identity the random effect. *Post hoc*, pairwise comparisons between treatments were made with Tukey's HSD tests. Additionally, we analysed the distribution of node types in the network by looking at the proportion of each individual node type in each network. The relative difference in proportions of node types across treatments was analysed using a two-sample *t*-test.

To eliminate the effects of colony-level variation on nest size and structure, dimensionless differences in nest length, excavated sand and nest complexity (as a number of edges) were expressed as ratios between treatment groups, within colonies. These relative differences in nest size and complexity are reported as means with standard deviations. Data were normally distributed and a single one-sample *t*-test was used to determine if dimensionless values were equivalent between treatments (reference mean $\mu = 1$, R package *stats*).

All data were plotted using R packages *ggplot2* and *ggjoy*. Network drawings were generated using the R package *igraph*. Nest images were prepared for figures using Microsoft Paint 3D v.1703. Accompanying data files (electronic supplementary material, S2), source code (electronic supplementary material, S3) and network drawings (electronic supplementary material, S4) are included in the electronic supplementary material of this paper.

3. Results

(a) Nest length and sand weight

Over 48 h, groups of 60 workers produced nests ranging from 10 to 137 cm in total length (figure 3a). Nest length differed significantly between treatments (LMM, ANOVA, p < 0.0000, table 1). The nests produced by a mix of large and small workers averaged 85 cm (s.d. 30) in length and were significantly longer than those produced by both small workers alone (48 cm, s.d. 31) and large workers alone (61 cm, s.d. 22; both Tukey HSD, p < 0.004; electronic supplementary material, S5). In effect, nests excavated by a mix of worker sizes were 2.64 (s.d. 2.11) times longer than those excavated by small workers, and 1.43 (s.d. 0.38) times longer than those excavated by large workers from the same colony. The nests built by polymorphic groups were not only larger in absolute terms, but 1.67 (s.d. 0.44) times longer than expected based on the summed contributions of each colony's large and small workers in isolation (LMM, ANOVA, *p* < 0.0000, table 1).



Figure 4. Distributions of (*a*) total number of edges in a network by treatment and (*b*) out-degree distributions by treatment as a function of the distance from the nest entrance.

Table 1. The influence of worker body size on nest length, excavated sand weight, observed and expected length, and weight were assessed with LMMs with colony identity as a random effect. The influence of worker body size on edge number was assessed with a Poisson-distributed GLMM, with a log-link function and colony identity as a random effect. Type II Wald χ^2 -tests were used to determine the overall significance of treatment in each model. Significance levels less than 0.05 are shown in italics.

fixed effect	estimate	s.e.	t/z	<i>p</i> -value		
nest length	$\chi^2 =$ 47.50, <i>p</i> ·	< 0.0000)			
(intercept)	47.67	7.32	6.51	—		
60 lg	13.44	5.85	2.29	0.033		
30 lg $+$ 30 sm	39.65	5.85	6.78	< 0.0000		
obs. versus exp.	$\chi^2 = 63.74, p$	< 0.0000)			
nest length						
(intercept)	87.32	7.02	12.45	—		
expected	- 32.93	4.13	-7.98	< 0.0000		
sand weight	$\chi^2 =$ 40.69, $p \cdot$	< 0.0000)			
(intercept)	12.55	2.86	4.39	—		
60 lg	12.53	2.47	5.07	< 0.0000		
30 lg $+$ 30 sm	14.67	2.50	5.87	< 0.0000		
obs. versus exp.	$\chi^2 =$ 11.91, $p = 0.0006$					
sand weight						
(intercept)	26.99	3.03	8.91	—		
expected	- 8.00	2.32	- 3.45	0.0022		
edge number	$\chi^2 =$ 20.20, $p \cdot$	< 0.0000)			
(intercept)	1.26	0.19	6.68			
60 lg	0.26	0.19	1.41	0.16		
30 lg $+$ 30 sm	0.72	0.17	4.23	< 0.0000		

The weight of the sand excavated by workers ranged between 1 and 49 g (figure 3*b*), and differed significantly among treatments (LMM, ANOVA, p < 0.0000, table 1). Small workers excavated an average of 13 g (s.d. 10), while large workers excavated 26 g (s.d. 9) over 48 h. Workers from the mixed-size treatment excavated an average of 27 g (s.d. 12), or 3.33 times (s.d. 3.0) more sand than small workers

within the same colony (Tukey HSD, p < 0.001). While they did not excavate significantly more sand than large workers alone, mixed groups dug 1.51 times (s.d. 0.49) more sand than expected based on the mean contribution of both single-sized worker groups in isolation (LMM, ANOVA, p < 0.0005, table 1).

(b) Nest structure and complexity

The networks representing each nest contained between 1 and 17 edges (i.e. between 2 and 18 nodes). Figure 4a shows the distributions of the number of edges in a network organized by treatment. The effect of treatment was statistically significant (Poisson GLMM, ANOVA, p < 0.0000). Networks produced by 60 small workers were not significantly different in size from those produced by 60 large workers (Tukey HSD, p =0.34). However, when the two worker sizes collaborated in the mixed-size treatment, the resulting networks were significantly larger than both those of only small workers alone and those of only large workers alone (both Tukey HSD, p < 0.0095, figure 5). Similar results hold when taking into account the possibility of colony-level variation. Nests built by mixed groups had, on average, 3.6 times (s.d. 3.0) more edges than those produced by small workers alone $(t_{12} = 3.14, p = 0.0086)$ and 1.89 times (s.d. 1.7) more edges than those produced by large workers in isolation ($t_{12} = 2.75$, p = 0.018).

The presence and abundance of nodes representing chambers and terminations were not significantly different between treatments, indicating that no single body size is responsible for building these particular features of the nest architecture. However, mixed-worker size groups produced a significantly higher proportion of nodes representing branches, when compared to both groups of only small workers ($t_{16.23} = -3.26$, p = 0.0047) and groups of only large workers ($t_{18.49} = -2.3$, p = 0.033) with, respectively, 1.98 times and 1.40 times more branching nodes. These results provide further evidence that the interaction between differently sized workers yields greater architectural complexity.

Across treatments and depths, branching tended to take the form of simple bifurcations. This result can be observed in figure 4*b*, where most of the probability mass of the out-degree distribution of nodes is represented by nodes with degree 2. Though not statistically significant,



Figure 5. A selection of casts showing relative nest size and complexity by treatment (size classes are indicated above) and colony identity (displayed to the left of each group of casts). (Online version in colour.)



Figure 6. (*a*) Large workers excavated more sand per centimetre than small workers (large y = 6.31 + 0.31x, $F_{1,11} = 11.03$, $R^2 = 0.46$, p = 0.0068; small y = -1.17 + 0.29x, $F_{1,11} = 34.21$, $R^2 = 0.73$, p = 0.0001) while mixed groups excavated an intermediate amount of sand per centimetre (mixed y = 6.29 + 0.24x, $F_{1,11} = 5.71$, $R^2 = 0.28$, p = 0.036). (*b*) Worker head width was a significant predictor of the amount of sand carried per excavation bout (y = -1.69 + 6.88x, $F_{1,30} = 20.93$, $R^2 = 0.41$, p < 0.0001).

nodes that produced more than two branches tended to be closer to the nest entrance and were only rarely observed at greater distances.

(c) Body size and excavation

Across treatments, nest length was a significant predictor of the weight of sand excavated per cm (linear regression, $F_{1,37} = 45$, $R^2 = 0.54$, p < 0.0000, n = 39 nests). The amount of sand excavated per centimetre was consistent with the average body size of the workers present, so that large workers excavated more sand per centimetre than small workers, while mixed groups excavated an intermediate amount (figure 6*a*). These results suggest that workers might use their body as a template to determine shaft width, rather than excavating shafts sufficiently wide for the entire range of body sizes within the colony. Although the overall amount of sand excavated by workers in the mixed-size treatment was intermediate between

that of large and small workers alone, the amount of sand excavated as a function of nest length increased more slowly in the mixed treatment. The slope of the line describing sand weight excavated per cm is similar between the large and small worker treatments (small workers: y = -1.17 + 0.29x; large workers: y = 6.31 + 0.31x), but is significantly lower in the mixed group (y = 6.29 + 0.24x). This decrease may be explained by the number of extra, concurrently developing shafts, which were not yet fully formed in the mixed-worker treatment.

In a separate experiment, we observed workers carrying between 1 grain and 15 grains of sand per excavation bout. Worker head width was a significant predictor of the amount of sand carried (figure 6*b*, linear regression: $F_{1,30} = 20.93$, $R^2 = 0.41$, p < 0.0001, n = 32 ants). On average, large workers carried 9 (s.d. 3) grains of sand per trip while small workers carried only 3 (s.d. 2) grains per trip (sample of 10 small and 12 large workers). While large workers frequently carried fewer grains than the maximum amount recorded for their

size class, small workers never carried large boluses and occasionally exited the nest facing backwards and dragging their loads. Body size is, therefore, likely to account for the significant difference in total weight of sand excavated by large and small worker groups in isolation (table 1). As in wild colonies [15], both small and large workers were observed depositing sand grains on the surface within seconds of one another in the mixed-size treatment (electronic supplementary material, video S1).

4. Discussion

Across social insect societies, worker heterogeneity has been demonstrated to influence colony performance, from the selection of better nest sites to increases in foraging duration [29-31]. In this study, polymorphic worker groups created longer nests, excavated more sand and produced greater architectural complexity than single-sized worker groups. The nests built by mixed-size groups were both larger in absolute terms and larger than expected based on the mean contribution of both size classes in isolation. The amount of sand excavated per centimetre was related to body size, but specific features, like chambers and nodes with numerous branches, were not produced by a particular worker size class or a combination of sizes. Instead, all workers generated the same basic nest components, and tended to excavate nests that branched more at shallow depths. In polymorphic groups, non-additive increases in nest length were most frequently associated with an increase in the number of simple bifurcations and the resulting increase in the number of edges across the network describing the nest.

In nature, body size range and frequency in *V. pergandei* vary considerably across seasons [14,15], populations [17] and with respect to colony identity [18]. Large colonies that invest more resources in reproduction experience the greatest seasonal reduction in worker body size, while producing the most workers annually. These colonies also tend to contain significantly fewer patrilines (4 or fewer, range = 1 to 9 fathers) [18]. Owing to the relationship between nest architecture and polymorphism, nests built in different seasons by colonies with different pedigrees may differ markedly in form and may also differ in function.

Because body size is related to multiple colony-level traits in *V. pergandei*, selection acting on features tied to worker body size, such as mating frequency and colony size, could also indirectly influence unrelated colony characteristics, like nest architecture. In honeybees, artificial selection on a colony-level trait, pollen hoarding, had downstream effects on numerous other aspects of the colony phenotype as well as underlying worker characteristics [32]. Likewise, nest variants that result from differences in intrinsic worker characteristics and increase colony fitness, could affect other levels of colony organization across generations in *V. pergandei*.

(a) Sources of variation

Further study is needed to determine why polymorphism influences nest architecture in *V. pergandei*. One possibility is that the physical interactions of differently sized workers allow for more workers to access the nest at one time. For instance, if traffic in the developing nest is limited by body size, variation in size might increase the number of workers that can occupy a developing shaft. Increased packing could also change the flow of traffic, allowing workers of different sizes to pass one another without stalling. Alternatively, extra digging faces and branching may appear if large workers push small workers aside during excavation, or if queuing time at an active digging face increases for one worker size class when the other is present [33].

In our polymorphic treatment groups, both size classes accessed the nest and deposited soil within seconds of one another (electronic supplementary material, S6) [15]. For this reason, the possibility of 'shift work' or a temporal division of digging by size is unlikely. We found that average body size predicted the amount of sand excavated per centimtre. Just as Lasius niger workers use their own body length as a template when placing roofs over columns inside developing nests [34], our results suggest that V. pergandei workers use their own body size to determine shaft width, instead of excavating shafts wide enough for the range of body sizes in their source colony. When both size classes worked together, they excavated an intermediate amount of sand per centimetre, but the rate of excavation per centimetre was lower than that of either monomorphic group. This may be attributable the additional shafts produced by the mixed treatment, which had not yet reached their final diameter. Therefore, we expect that completed shafts accommodate the largest size class present, rather than being intermediate in size.

Social insect colonies are known to have daily behavioural rhythms, and it is common in the laboratory to see pauses in digging activity while large groups of workers engaged in allogrooming or feeding. We did not measure overall and individual activity levels across different treatment groups in our study, but detailed video and tracking of individuals in different contexts may reveal any individual or group-level changes in motivation or overall activity across treatments. In other ant species, a significant amount of excavated material is cached below ground and transported upward in different stages when space is needed, often by multiple, age-correlated worker groups [13,27,35]. Our study design did not allow for observation of below-ground deposition, but it is possible that polymorphic groups were more motivated to remove cached sand or that one size class tended to remove cached sand when the other size class was present.

Although nest size and complexity differed significantly across treatments, similarities in relative complexity were also apparent within colonies (figure 5). For instance, when single-sized worker groups produced large or more complex nests in isolation, the nest produced by both worker types in combination often appeared larger or more complex than others in the same treatment. Since treatments were run concurrently for each colony, it is possible that equivalent nutritional and experiential status influenced the activity levels of workers across all colony members. Alternatively, intrinsic genetic factors may have contributed to the overall behavioural algorithms of workers across size classes. In V. pergandei, adult body size is related to juvenile nutrition rather than patrilineage within colonies [18]. Therefore, it is likely that within colonies, genetic structure was equivalent across treatment groups and could underlie some of the similarities observed across size classes.

(b) Natural nest architecture

The intention of the present study was not to describe the natural nest architecture of *V. pergandei* colonies but to highlight the individual and synergistic contributions of worker morphology to nest excavation while holding all environmental factors constant. Having established the non-additive effects of worker body size on nest size and architecture, future work can explore the relative influences of body size under additional organizational and environmental conditions. Like other ant species, V. pergandei workers experience carbon dioxide [36], moisture, temperature and soil hardness gradients across the vertical strata of the nest, which may span several metres [9,19]. Across their range, V. pergandei appears in diverse soil types, from pure sand dunes in the Anza-Borrego Desert to mixed gravel and fine particulate alluvial soils of central Arizona, which may have profound effects on the structures they build. Moisture is also a key feature affecting nest development in ants [6]. Although V. pergandei colonies have been observed excavating new nests in all seasons, surface soils only contain substantial moisture during the brief monsoon season, and the pronounced slanting of this species' natural architecture may be a response to the risk of collapse in dry soil.

Although the nests examined in the current study were incomplete and dug in laboratory buckets, they did share characteristics of the partial nest cast by Tschinkel [9] in the Anza-Borrego Desert, including wide central shafts with numerous ancillary shafts branching outward as well as flat horizontal chambers. Unlike the cast of a mature colony, nests that developed over 48 h lacked numerous tunnels with high connectivity below the surface [9]. In other harvester ant species, the top of the nest is occupied by recruitable foragers [28,37] and serves as a depot for incoming seeds, outbound sand and waste [38], as well as sites for warming developing brood. It is likely that these complex, near-surface structures develop in occupied nests over time or in response to particular stimuli. In Acromyrmex lundi, for example, the presence of fungus and brood determines the architecture of developing chambers [8]. Likewise, in the seed harvesting ant P. badius, both chamber density and complexity are associated with increasing worker number across colony ontogeny [10].

(c) Possible benefits of polymorphism

In V. pergandei, worker body size does not influence the size of seeds an individual collects, or the tendency of an individual to participate in nest excavation and foraging behaviour [15]. One clear outcome of polymorphism in our study was a relative increase in the rate of new nest growth. In xeric habitats, reducing exposure to surface temperatures by excavating a larger nest more rapidly could increase individual longevity, which averages just 18 days following the onset of foraging [18]. Many other colonylevel characteristics of V. pergandei depend on avoidance of desiccation [39]. For instance, the risks of heat and desiccation drive colonies to shift their foraging schedule to pre-dawn hours during the extreme heat of summer [40]. Unlike other members of the genus, and most other Sonoran desert ants, V. pergandei mating flights occur during the comparatively mild temperature window between February and March, rather than at peak temperatures during the late-summer monsoon season [41]. Even under these conditions, cuticular abrasions suffered while digging can lead to desiccation and death of new queens [43].

Our experiment loosely simulates the initiation of a new nest pioneered by a small group of foragers and the results suggest that polymorphism expedites nest deepening, which may represent another adaptation to desert living in mature colonies. Polymorphism may also benefit colonies earlier in their ontogeny. After founding a new nest, queens produce an initial cohort of tiny, monomorphic workers. Average worker size increases for up to a year with each successive cohort [15,41]. During this time, colonies that develop polymorphic workers early on may be able to relocate nests more quickly in response to competitors or environmental factors.

Although the experimental design differed, a similar study of polymorphism in S. invicta compared tunnel area between worker size classes in a quasi-two-dimensional arena filled with wetted glass particles [11]. Control groups, composed of a random sample of the natural size frequency in each source colony, only excavated significantly more tunnel area than large workers in isolation. In contrast to Gravish et al. [12], we found that mixed-worker groups excavated longer nests than both small and large workers in isolation, but that small workers alone excavated significantly less sand than other treatments. It is unclear whether the excavation abilities of large S. invicta workers were limited by the twodimensional digging space or represent the natural tendency of workers with different body sizes to perform specialized tasks [42]. Our study took place in three-dimensional space that allowed workers to build structures in any plane, move and interact without physical constraints. We also equalized the ratio of large to small workers in each experimental group, while in the study of S. invicta, small workers were the most common size class present in control samples, which may account for the similarity between nests built by small-only and control groups. In either case, determining the ratio of large to small workers necessary for a polymorphic group to outperform a monomorphic group would provide additional insight into the benefits of excavation in specific seasons for V. pergandei colonies.

5. Conclusion

Social insects modify their environment by building nests. These nests serve numerous important functions for the colonies living within. Each colony's nest architecture is both the result of collective behaviour and a device that can shape collective behaviour [44]. In this study, we used a cross-disciplinary approach to analyse how seasonal and colony-specific variation in worker polymorphism influence variation in nest architecture. Worker groups containing more than one body size produced larger and more complex nests, demonstrating that worker interactions can have non-additive outcomes distinct from those of component worker types in isolation. By increasing nest complexity, polymorphic worker groups excavated larger nests, more rapidly. The interplay between colony genetic architecture (matriline and patriline numbers), seasonality, worker body size and nest architecture has not been considered previously among ants. Our findings suggest that selection on multiple colony-level traits in V. pergandei could influence body size frequency distributions, which in turn, characterize both annual worker production and nest architecture.

Data accessibility. Datasets, source code and additional images supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. C.L.K. designed the study, collected field and laboratory data, analysed the data, participated in figure design and

9

drafted the manuscript; G.V. managed the data and accompanying code, conducted the formal analysis, designed the figures and drafted the manuscript; B.H. participated in the design of the study, edited the manuscript and provided support for this project. All authors gave final approval for publication.

 $\ensuremath{\mathsf{Competing}}$ interests. The authors of this study declare no competing interests.

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Visualizing aggregate movement in cities

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We argue here that despite the focus in cities on location and place, it is increasingly clear that a requisite understanding of how cities evolve and change depends on a thorough understanding of human movements at aggregate scales where we can observe emergent patterns in networks and flow systems. We argue that the location of activities must be understood as summations or syntheses of movements or flows, with a much clearer link between flows, activities and the networks that carry and support them. To this end, we introduce a generic class of models that enable aggregated flows of many different kinds of social and economic activity, ranging from the journey to work to email traffic, to be predicted using ideas from discrete choice theory in economics which has analogies to gravitation. We also argue that visualization is an essential construct in making sense of flows but that there are important limitations to illustrating pictorially systems with millions of component parts. To demonstrate these, we introduce a class of generic spatial interaction models and present two illustrations. Our first application is based on transit flows within the high-frequency city over very short time periods of minutes and hours for data from the London Underground. Our second application scales up these models from districts and cities to the nation, and we demonstrate how flows of people from home to work and vice versa define cities and related settlements at much coarser scales. We contrast this approach with more disaggregate, individual studies of flow systems in cities that we consider an essential complement to the ideas presented here.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction: defining movement

Patterns of human movement have been explored from classical times but it required a revolution in technologies which began with the industrial revolution to raise their prominence to systematic study. It was the internal combustion engine and mechanical vehicular technologies that developed in its wake that enabled cities to grow beyond the constraints imposed by how far we could walk which tended to limit the biggest cities to populations of less than a million. However as soon as the railway developed in the early nineteenth century, the ways in which people could move using such technologies became significant, not only because people could travel much further but because they could restructure their lifestyles in terms of where they lived and worked. One of the earliest descriptions of such patterns was made from a survey of all movements of traffic in the Pale of Dublin in the 1830s by the British Army. In 1837, Lieutenant Henry Harness produced a visualization of the flows within Pale which was the effective hinterland of Dublin [1] and his map provided a portent of things to come. The survey was specifically designed so that the British Government could figure out if there was enough traffic to build a railway, and these kinds of visualization are now used routinely to explore the impact of new transportation infrastructure. Many of the flow maps presented in this paper follow in Harness tradition including the famous

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2

map produced by Charles Minard in 1869 of the increasing and thence decreasing strength of Napoleon's army as it made its way to and from Moscow in 1812–1813 [2].

Human movements are initially recorded at the individual level and there are many plots of individual trajectories, as, for example, in very local contexts such as games where motion is key to the way the individual plays the game or the way a team confronts another on the field. The patterns produced by these kinds of situation often display aggregate structure and thus analysis has begun to explore aggregate trajectories and trails in search of a more generic spatial logic. In the case of cities, this is easy to see in terms of daily flows from suburbs to city and more locally with respect to retailing, which represent the predominant people and materials flows that are formed from the way contemporary cities have developed radially and concentrically around a central core. Our focus here is thus on spatial patterns that are aggregated from individual movements. Therefore, we will not present, explain or simulate the sorts of patterns and behaviours associated with fine spatial scales such as large-scale entertainment events where crowding is key. We will not discuss models of how individuals react to one another and their environment in generating emergent patterns, nor will we discuss the kinds of negative and positive feedbacks that determine how such patterns emerge. Our focus is thus on representing the patterns and visualizing their complexity in physical terms which can be clearly visualized in 2- (and 3-) dimensional Euclidean space, the key metric used by those disciplines and professions that aim to understand and then plan the built environment. We elaborate the wider implications for cities elsewhere [3].

There are many other perspectives on human movement that do not emphasize the kind of physicality that we assume here. Movement is intrinsic to the way people behave and even if they do not move physically, many social and economic relationships which tie individuals together imply communications that explain how individuals are positioned and located in space. For nearly 100 years, the social sciences have sought to explain power relations using networks while markets that define the way individuals and groups engage in exchange, trading with one another, imply the transfer of materials, money, and ideas. In fact, most social relations do invoke physical movement at some stage but in many discussions, this remains implicit. For example, the recent growth in network science has not focused very strongly on networks embedded in physical space for social networks which have driven applications are essentially topological and relational [4]. Here we will take the opposite approach rooting our presentation in explaining and visualizing patterns of movement that take place in physical space, often ignoring the detailed rationale for movement but always aware of the fact that our approach needs to be complemented by many other perspectives. In fact, the city is a many-facetted object or system of study and it is unlikely that there will ever be any comprehensive theory that relates all its dimensions. It is the example of a complex system par excellence [5] where a complete explanation of its form and function depends on many disciplines and scientific approaches.

The last feature of our study of movement which we need to emphasize relates to spatial scale. Although all the trajectories that we assemble here are traced from individual spatial behaviours, our two examples-from the multitude that we could envisage-aggregate these traces into patterns that are associated with intense dis-contiguous hubs in the city such as stations or districts where the populations are aggregated into at least the hundreds, sometimes the thousands. What we assume but do not have time to explain here is that if we were to disaggregate these to finer spatial scales, we would begin to see very different patterns for although there is a degree of self-similarity in cities as explored in the idea of the fractal city [6], explanations of urban phenomena, particularly movement patterns, differ at different scales. We do not have a good theory of how the many different kinds of patterns displayed at different scales can be integrated in a consistent set of explanations although we consider the purpose of this special issue of the journal is to assemble many different perspectives on such individual and collective phenomena; and we assume that this issue will enable readers to get some sense of the challenges in integrating different viewpoints and charting a way forward which enables us to integrate these ideas more effectively.

2. Locations and interactions

In this paper as we have already implied, we treat cities as large agglomerations of individuals who cluster together to pursue social and economic tasks to their mutual advantage. This advantage is defined as economies of scale which arise when individuals pool their labour and support their community with social relations. Cities are thus the hotspots in the economy, central to the way production and consumption are organized. Our usual model of their form is physical which we define at different spatial scales from the location of buildings at fine granularity through to entire metropolitan areas or regions whose morphology is much more coarsely configured. Since classical times, whenever there has been debate about cities, their representation has usually been in physical terms which we have come to call spatial where location and place are the key determinants of urban structure. Although cities evolve through time, most of our thinking about their form has been as if they are in equilibrium. They have been primarily explored at cross-sections in time while their dynamics has been, at best, implicit, largely because of severe limits on our ability to observe them in the aggregate or even at the level of individual behaviour over time.

Cities are thus primarily studied starting from their physical representation either at the scale of buildings which is essentially architectural or at the scale of the complete system, the entire town or metropolis which is essentially geographical. There is a strong disciplinary divide between these two perspectives which is reflected not only in what is articulated but also how their study takes place. At the finest scale, cities are essentially sets of buildings where the focus is on the building use, construction and design. In contrast at the city scale, the focus is on how different locations relate to one another in terms of their uses, their densities, and who and/or what occupies those locations. These may be anything from street addresses at the fine, small-scale to administrative units such as census tracts at the coarse, larger-scale. Thus the focus at the smallscale is essentially architectural and also possibly through

3

the lens of engineering while at the large-scale, it is socioeconomic. In this paper, we will select examples from each of these scales to give some sense of the main issues involved in questions of how their components—buildings to locations—relate to one another.

Here we will not be emphasizing the raw physicality of buildings and locations per se, for the study of cities is fast moving away from these perspectives to explaining how cities function in terms of patterns of movement. To this end, we need to begin to think about buildings and locations other than with respect to their autonomous representation but in terms of how they relate to one another. In this perspective, location no longer takes pride of place, it is the relationships between locations that are critical. In this sense, location can be seen as being a function of these relationships. The best example one might point to is residential housing. At any time of the day, the number of residents in any location will vary and this variation depends on the numbers who travel to or from the location in question for different purposes such as employment, education, retailing and so on. It is not really possible to explain the numbers at such a location without understanding these relationships that determine how many people reside, work, shop, go to school and so on in every other location. In this sense, then, we might think of locations as being functions of interactions or movement, of which there are many types, some spatial but some acting in non-spatial ways through electronic or social media. In any event, we treat these interactions as spatial aggregates where we see the clearest patterns emerging from individual movements associated with activities which ultimately are generated from the bottom up.

Although we have noted that cities tend to be studied and represented as though they are in equilibrium, movement in and of itself implies change and dynamics. Movements take place in time-they operate through time-but they also change on slower time scales just as the occupation of buildings and locations change with respect to their use and density. For the most part, here we will not study very long-term changes in movement but we will point to some of the research questions that need to be explored. Our problem in extracting the study of movement from the study of the city more generally is that our theories about cities are not well-formed and often confused-there is a science in the making but this is rudimentary [7]. We thus have to curtail our discussion of certain aspects of movement due to the fact that we are not able to discuss dynamics and equilibrium in great detail or questions about the evolution of cities and their complexity. Nevertheless, we will provide a rounded enough review to hopefully engage the reader in some of the key questions.

The current changes in our thinking about what is happening with respect to the study of location and movement in cities arises from many issues. First, it is logical to suppose that objects which are related to one another cannot be satisfactorily explained and understood without considering the set of relations within which those objects are embedded. Second, our current practice of design and planning has clearly demonstrated over the last century that simply assuming we can rebuild our cities without taking relationships between the objects that comprise them is wholly inadequate. We now know enough about cities to know that if we ignore how things are connected to one another, particularly with respect to their transport, all sorts of counterintuitive and undesirable effects can occur. The classic example is the problem of observing traffic congestion on a highway and then deciding to enlarge the road or build another in parallel to reduce the current flow volumes, only to find that both roads fill up with traffic as soon as the increased capacity becomes available. Interdependencies are everywhere in cities and we ignore them at our peril. Third, as we move headlong towards a digital society, many new patterns of movement through electronic transmission have come to dominate our cities. Email for example, now underpins most economic and a good deal of social activity, and social media is influential on what and where we do things in cities but so far it is largely a closed book with respect to the effects it is having on how are cities are organized. The substitution and addition of an online world alongside our material world is having enormous effects but we have little idea of what these are because we do not have good models to understand the importance of movement. All this raises important challenges that need to be resolved to enhance our understanding of how cities form and function.

There is one other important issue pertaining to a science of cities that we need to note before we focus on movement and this relates to measurement. In the past, most science has achieved its goals by defining systems as sets of objects that are subject to extensive and continually improving measurement. This has also been a precursor to good classification. When we enter the world of relationships between objects, it has been much harder to develop satisfactory measurements, largely because relationships are harder to define and harder to abstract. Relationships are less stable and even if they pertain to flows, these vary in time and hence are harder to identify. Capra & Luisi [8] have articulated this problem rather well and point to the difficulties of understanding relationships between objects in very clear terms when they say:

The shift of perspective from objects to relationships does not come easily, because it is something that goes counter to the traditional scientific enterprise in Western culture. In science, we have been told, things need to be measured and weighed. But relationships cannot be measured and weighed, relationships need to be mapped. (p. 80)

In this paper, we will take Capra & Luisi [8] at their word and demonstrate how movements need to be defined not only formally and through data but also in terms of their visualization. We will in fact map physical movements quite literally as cartographic patterns but also in terms of other ways of showing spatial relationships. Before we launch into models and methods for doing this however, we need to define how we might best represent movement in cities and to this end, we will define the wider domain in which such relationships exist.

3. Representing flows and networks

We will assume that cities can be represented as a set of locations whose attributes we will denote using indexes i and j where we assume that these pertain to locations that have an area such as a census tract or a point such as an address, geocode or geotag. These locate a point where a building is centred or the centroid of an area which contains some activity of relevance to the spatial system in question. We can identify at least two kinds of attribute that relate to movement: F_{ij} which is the flow volume of activity or

4

information between *i* and *j*; and σ_{ij} which we define as the channel or network link between *i* and *j*. The network link might be measured as being present $\sigma_{ij} = 1$ or not $\sigma_{ij} = 0$ or it may have some attribute pertaining to its physical channel capacity etc. If we measure capacity as q_{ij} , then it is easy to see how we might define the flow density as $\partial_{ij} = F_{ij}/q_{ij}$.

These kinds of measurement are easy to make for material flows such as road traffic but for electronic they are much harder to observe. For social relationships as developed in studies of social power, neighbourhood association, and personal/cognitive interaction, they may well be almost impossible to define, notwithstanding that there is widespread agreement that they exist. Indeed, there are important contributions to understanding how cities work that do not refer explicitly to physical flows such as in the work of Lefebvre [9] among others and a rounded view of urban phenomena must embrace these related perspectives as we alluded to earlier. However, in measuring relationships where flows and networks are relevant together, then measures are often mixed, flows being based on people, or packets, or materials while networks pertain to the physical characteristics of channels. In one sense, flows pertain to activity locations while channels pertain to the physicality of the environment in the same way buildings are defined. This mixture can be confusing and one has to exercise great care in combining and comparing interactions which involve both flows and their networks as conceived in terms of channels.

We must first make two sets of distinctions between short and long time scales, and between fine and coarse spatial scales. Different kinds of movement take place across different types of space and over different time intervals, and this is further complicated by the fact that movements that occur frequently over short time periods might also change their form and function less frequently over longer time periods. The same is true for movements across spatial scales in that movements that take place, let us say within a building on a real-time basis, might change and can then be aggregated up to the neighbourhood scale. Many changes across these scales involve changes which show themselves in the individual elements at the finest scale. Again this can be potentially confusing because movement takes place in real time in any case and it is only when we aggregate it over space and time do we see different patterns across these scales. It is when these patterns change over longer time scales that we can better detect variations at more local spatial and temporal scales.

We need to make a simpler distinction with respect to time scales. In terms of time, we can define what we will call the 'high-frequency city' and the 'low-frequency city'. The high frequency is the city that contains movements that occur in real time and can be observed in real time or near real time such as the movements of individuals or emails or energy flows that can be monitored and aggregated from seconds to minutes to hours and even to days, weeks and months. Beyond this, we are really dealing with the lowfrequency city where months turn into years and where years add to decades, centuries, epochs, eras and so on. Typical differences might be between journeys made during the working day such as the journey to work from home compared to residential relocations that take place over years. To an extent all movement takes place in real time and the difference between the high- and low-frequency city is

really one of how clear the patterns are at these different frequencies. The same kind of distinction takes place over spatial scales. At the finest scale, we are probably talking about people movements in terms of walking which define the scale at which these are recorded in contrast to transit movements that take place over wide areas such as the entire city region. In terms of temporal scales, movements are usually recorded second by second, or minute by minute or even hour by hour from real-time sensors but further aggregations tend to be generated from the finest real-time observations. When movements are recorded over months and years and decades, the actual movement is in real time but its aggregation is to much bigger temporal units. Spatial scale tends to be the focus of interest for all movement as it is recorded at the basic level although its aggregation to different spatial scales is usually based on what the focus of interest is, high frequency, small scale or low frequency, large scale which define the two key poles of interest in cities. We will use this simple classification to organize the presentation of our two demonstrations which follow.

In the last one hundred years, the main networks that have come to describe cities have been those based on transportation with road, rail, bus, walk and cycle modes being the most obvious and often sharing common physical infrastructure. Material flows which use these networks have also been separated from people flows but flows of information such as telegraph messages and telephone calls have barely been charted since their inception, notwithstanding early efforts to describe their significance to the form and function of the city [10,11]. Until the 1960s, computers were not generating flows of information in anything other than at the most local scale of the machines themselves and their off-line users but with the emergence of the Internet from that time on, email began to grow. With the development of the web, search, hand-held devices, and social media since the late 1990s, dramatic amounts of information are now circulating around cities which are probably having a major impact on many traditional patterns of location. All of these flows are pictured more with respect to their networks than the volume and capacities of their flow systems. To an extent, flows and networks are different sides of the same coin-one cannot exist without the other but it is the measurement of flows that is the most problematic, largely because of the invisibility of this data. Over longer periods of time, we can observe changes in where people live and work-changes which are implicit in migration patterns, and in measures of economic activity such as house prices and income and so on, all of which imply a degree of change, hence movement but in a non-spatial sense. The spatial dimension merges into the non-spatial when it comes to cities and this too reveals how complex the structure of the city is with respect to its dynamics and the way its economic markets interact with one another

In terms of data, physical networks are the easiest to observe with the growth in network science spurred on by the fact that many such networks are available for analysis. Flows are much harder to record. These have to be gathered using questionnaires which are expensive or by closed and robust automatic systems such as those used for recording transit payments. Many of the automated flow recording systems, beginning with analogue systems for recording flows of vehicles on roads, for example, cannot be integrated with data pertaining to those who generate these flows—the users—and hence the data, although accurate, is limited in its interpretability. Much data that would be useful such as electronic flow data e.g. email is largely invisible. It is so voluminous that even those who control the means of its distribution—the telecommunications companies—find it near impossible to make sense of the data for analyses that are important to their own study of movement for commercial purposes. Data on utilities is easier to measure but again invariably lacks any referent to use and where there is the prospect for such usage data as in the flow of electricity and related energy flows, making sense of these in socio-economic terms is limited.

Various models of flow and network systems have been proposed and we will note some of these below but much depends on the nature of the movement, the scale of resolution and the kind of data that is available from which a model might be estimated. Models of individual flows at the finest spatial and temporal scales have been proposed and many of the other papers in this special issue deal with such models. These are often referred to as agent-based in that each individual or object that is subject to movement is identified as a relatively autonomous agent and the simulation proceeds by modelling each agent's decision with respect to why and how they move. Often actual data for such models is sparse or lacking and thus many of these models tend to be exploratory and indicative rather than predictive. At the coarser scale, aggregations of individuals into populations is the focus of models at the metropolitan city scale and these tend to be less acquisitive of data and thus easier to estimate. We will introduce these below. Moreover, an increasing number of models which are taken from real-time data on movement are descriptive rather than predictive. The range of models and their mathematics is quite wide and we will selectively illustrate examples below to give some sense of the range of model types.

We also need to introduce methods for making sense of both movement data and models. This is increasingly the domain of visualization and as a prelude to this, we will illustrate some of these for patterns of movement in Greater London at relatively coarse spatial scales. Given a set of origins and destinations between which spatial movements take place, we can first visualize these as a set of flows that take no account of the physical networks on which such flows are based. These we show for the journey to work in figure 1a which is based on the coarsest aggregation into London boroughs which we call 'zones' while the underlying much more detailed road network is shown in figure 1b. If we then assign these flows to the network, we generate pictures of network flows as in figure 1c for the road system and in figure 1d for the Underground (subway) system. There are two problems with these visualizations and both relate to the level of detail needed. The self-flows, that is, the flows that remain within the zones which are called intra-zonal, are often much bigger than the inter-zonal flows that is $F_{ii} \gg F_{ij}$, $i \neq j$ and these are visualized in the flow map in figure 1e. The other problem involves the level of detail of the spatial system in that as we increase the number of origins and destinations, the denser and more complex the data becomes and the more difficult it is to visualize. Figure 1a is a complete mess even for only 33 origins and destinations and therefore we need to simplify such flows. To resolve such problems of visualization, we need to move beyond a complete representation of each flow in map form and one way

of doing this is to produce the vector fields that we show in figure 1*f*. These are weighted directional flows which are an average of all flows from particular origins to all destinations. This simply gives some of the tools that are necessary to make sense of movement data and to provide some idea of these challenges, we will now explore two examples in much more detail.

Last but not least, we need to make the point that in the models and data we are focusing upon, the behaviour is that of the individual not the physical system that this behaviour is contained within. Individuals which represent our basic objects or components that make up cities do not influence the configuration of space at least in terms of the high-frequency city. Over longer time spans, individuals may adapt their behaviour to the physical structure of the city or vice versa adapting the physical structure to their own behavioural needs but we will not deal with the latter models here. The models we will focus on enable us to predict movement largely at a cross-section in time-as if the city is in equilibrium even though we know it is not [12]and we will emphasize how individual behaviours are aggregated to more macro types of behaviour in developing models at ever coarser spatial scales. Many of the models in the papers in this special issue deal with how the very local environment might be adapted by agents, particularly those that pertain to animal populations, but once we scale up to the city level, most individuals moving in cities at that level take their physical environment as fixed.

4. Movement in the high-frequency city

We begin with an object k which in our context is an individual or an aggregate of individuals engaging in movement for which we can define a probability p_{ij}^k of that object or aggregate moving from one location to another. We refer to the first location as an origin i and the second as a destination j and we define the probability for that object moving as

$$p_{ij}^k = \frac{\exp^{U_{ij}^k}}{\sum_z \exp^{U_{iz}^k}},\tag{4.1}$$

where U_{ij}^k is the utility gained which is associated with the movement by *k* from *i* to *j*. The utility is usually defined as a weighted linear sum of benefits and costs associated with the spatial separation between and the activity located at the origins and destinations of the flow. Here we will specify this as a benefit W_j^k at location *j* and a cost of travelling c_{ij}^k from *i* to *j*. We can aggregate across individuals or specify costs and benefits as aggregates of individuals although in terms of our first example involving movements at different times of the day, we will restrict our models to those simulating individuals. Using these definitions, our model thus becomes

$$p_{ij}^{k} = \frac{\exp^{\alpha^{k} W_{j}^{k} - \beta^{k} c_{ij}^{k}}}{\sum_{z} \exp^{\alpha^{k} W_{z}^{k} - \beta^{k} c_{iz}^{k}}},$$
(4.2)

where the parameters α^k and β^k are determined so that the model fits observed behaviour in some best way. Finding a best fit for these models is an enormous subject area well beyond the scope of this paper just as the generalization of these models to wider developments in theories of choice opens the door to invoking ideas about individual perception



Figure 1. Different visualization of flow systems for Greater London. (*a*) Direct flows: desire lines; (*b*) London's road network; (*c*) flow assignment to the road network; (*d*) flow assignment to the subway network; (*e*) non-spatial direct flows; and (*f*) averaged vectors based on weighted averaging of direct flows. (Online version in colour.)

of the utilities involved in undertaking movements of any kind [13,14]. In equation (4.1), the probability is defined with respect to the individual and thus it is a conditional probability of being located in *i* and moving to *j*. If this probability pertains to a larger group of individuals, then we can write the flows F_{ij}^k associated with the movement probability as

$$F_{ij}^{k} = \frac{O_{i}^{k} \exp^{\alpha^{k} W_{j}^{k} - \beta^{k} c_{ij}^{k}}}{\sum_{z} \exp^{\alpha^{k} W_{z}^{k} - \beta^{k} c_{iz}^{k}}},$$
(4.3)

where O_i^k is the total number of individuals being aggregated into a class or group *k*. Note that this probability is normalized to this total if summed over *j*. If the utilities pertain to individuals rather than a group, then we can write the total flow for all groups as

$$F_{ij} = \sum_{k} F_{ij}^{k} = \frac{O_i \sum_{k} \exp^{\alpha^{k} W_{z}^{k} - \beta^{k} c_{ij}^{k}}}{\sum_{z} \exp^{\alpha^{k} W_{z}^{k} - \beta^{k} c_{iz}^{k}}}.$$
(4.4)

The summation over j gives the total of all individuals moving from origin i to all destinations j as O_i .

There are many variants of these models that are adapted to different flow systems, but two classes stand out that are closely related. Their origins lie in analogies with gravitation and potential and were proposed as far back as the late seventeenth century just after Newton developed his basic mechanical equations. In the 1960s, these models were reinterpreted using ideas from statistical mechanics that provided a formal structure for their derivation as entropymaximizing models [15]. They are still widely applied in transport modelling. In the 1970s, they were disaggregated and linked to individual-choice theory [13], and this provided a basis for much more detailed individual modelling [14]. These discrete choice models have been further developed to underpin a variety of micro-simulation models of transport activity such as the MATSim model [16], and as embedded in these kinds of agent-based activity frameworks, they now constitute the state of the art. Currently the limitations of



Figure 2. Travel volumes and profiles for the Underground (subway) in Greater London. (*a*) Abstracted flows within central and inner London; (*b*) exits and entries across the entire system; (*c*) daily trip volumes in all subway stations; and (*d*) morning, evening peaks and football matches at the Arsenal subway station during a synthetic week.

these models with respect to the factors used by individuals to articulate travel costs are being addressed but progress is slow and faces the same kinds of problem which dominate choice theory in general.

We will sketch as our first example two applications of these kinds of models to individual travel behaviour. In essence, we assume that the benefits of making a trip from an origin to a destination depend on what is at the destination which we measure by W_j^k which for the journey to work would be employment or some variant thereof such as wages while the deterrent effect or disutility might be transport cost c_{ii}^k . Note that the way these enter the utility function relates to their positive and negative effects on the amount of travel behaviour. In a system of origins and destinations, we can aggregate the individual flows to form the number of individuals at the origins that we assume we know and those that are predicted at the destinations. Now we need to build the model so that we can simulate the flows at different instants of time and in this sense, we have several variants of the basic model. We first annotate the flows by the time instant *t* as $F_{ii}^k(t)$ and we can specify utilities that vary with time too. Let us assume the most detailed model from equation (4.3) which can now be written as

$$F_{ij}^{k}(t) = \frac{O_{i}^{k}(t)\exp^{\alpha^{k}(t)W_{j}^{k}(t) - \beta^{k}(t)c_{ij}^{k}(t)}}{\sum_{z}\exp^{\alpha^{k}(t)W_{z}^{k}(t) - \beta^{k}(t)c_{iz}^{k}(t)}}.$$
(4.5)

Using the basic model in equation (4.3) where we have $O_i^k(t)$ individuals of type *k* at the origin, then we have a total at each

origin which is fixed as $O_i(t) = \sum_k O_i^k(t)$ and an activity or population predicted at each destination $D_j(t) = \sum_{ki} F_{ij}^k(t)$. We can then compare these predictions at the destinations with those that we observe from data, having calibrated the model using an appropriate method as we implied above [14].

Our first application is to movements on the subway system in Greater London where we have excellent flow data from the Oyster card system which is used by 85% of all travellers using the network and where the order of magnitude of trips just on the subway made during a working weekday is around 6 million. Each movement is captured by the data and made available on a minute by minute basis which can be further aggregated into any appropriate but larger temporal unit. The data can be graphed in terms of desire lines between origins and destinations where each line pertains to the number of trips [17]. We show an example of this for a typical peak hour in figure 2a. Each origin is shown in terms of the total flow in this figure while in figure 2*b* we show the breakdown into origin and destination flows as proportional circles and their subdivision into these two types-entries and exits-for each hub that is a subway station. In figure 2*c*, we show the typical flow over time for the whole system. In figure 2d, we show a subway station (Arsenal, adjacent to the Emirates Stadium, where Arsenal FC play). The flows during the typical working weekday are dominated by morning and evening peaks but the extremely peaked flows are due to trip makers entering and leaving the station associated with football games. In this figure, we use a convention where we graph the exits from

7

the subway station as positive net flows and the entries as negative.

We will not dwell on how we calibrate this model but there are many issues involving how the independent utility variables vary over the temporal intervals. Our goal here is simply to give the reader some sense of how we go about representing and modelling this kind of individual-based activity that can be easily aggregated to the system with which it is associated-a highly organized subway system with limited exit and entry points which has a very rigid physical configuration that forces behaviour to follow certain channels. Although there are many issues with this style of modelling, in this context it is the nature of the spatial system that has the most impact on the quality of these models. Such systems are highly constrained in that they are embedded within other transport systems that link different modes together. Many people travelling on transit systems such as the London Underground, also use less constrained transit and private transport systems as part of their overall patterns of movement. Trip makers must always walk some distance to gain access to a vehicular system and this kind of multimodal transport complicates the modelling process. It is possible to extend the models illustrated here to deal with more than one network and to enable networks to compete for the patronage of an individual traveller through different transport cost structures. One problem however is that data on multimodal trips is hard to assemble because different modes are captured in different ways. If the data is assembled by direct questionnaire, then there is some hope for comprehensive models but many new datasets such as the Oyster card system in London vary across different modes of transport. A traveller may use bus and subway and heavy rail to make a trip, and on each mode the use of the card differs, being comprehensive at both ends of the trip for subway, only being used to log the start or origin of a bus trip and varying dependent on the status of the users as to whether the card can or cannot be used on heavy rail. Walking between and to various transport modes depends on non-automated data which is hard to get although in time, some of this data might be acquired by automation using smart phone technology, subject of course to important limits on privacy and confidentiality. These then are some of the problems that plague these kinds of applications.

We noted above that the discrete choice models we have introduced here can be used to compute the probabilities of individuals making different kinds of trips during any period of time. These models treat individuals as agents and enable the sequence of origins and destinations that take place when individuals travel to be simulated. Essentially, each individual has a travel profile and time budget that needs to be met in terms of their daily activities. An individual will then generate trips to satisfy their daily activities schedule, and this leads to these trips being assigned to the network. Where they travel to is dependent on predictions from the models noted above, and these predictions are used to generate all the travel decisions during each individual's activity schedule. When all these trips are loaded (assigned) to the various networks, it is likely that the pattern is not feasible in certain ways and this leads to positive feedback that enables the individual traveller to make marginal changes in their schedules and locations that lead to another allocation. These changes hopefully lead to a convergence, hence a feasible pattern of trips which represent the solution.

These models generate individual movements and hot spots of congestion while also generating trip volumes in aggregate at different locations as computed from models such as that in equation (4.5). We have built such a model for Greater London using highly disaggregate household data, which enables us to predict journeys to work over typical daily schedules [18]. An illustration of this kind of simulation is presented in figure 3 but to examine this in the requisite temporal detail, readers are directed to view the Vimeo movies: MATSim for London at https://vimeo.com/ 119354430, and TRANSIMS for Milton Keynes, UK at https://vimeo.com/33108792.

5. Movement in the low-frequency city

We now need to move to more aggregate spatial scales where we also deal with aggregated populations but before we do so, we need to note the generic nature of the models we are developing. The model types that we have introduced with their links to highly disaggregate agent-based simulations based on individual behaviour, or to social physics/spatial interaction models of aggregate populations, are of similar form and structure. However, when one disaggregates to really fine spatial scales such as the level of individual streets, these models become less appropriate, and models that rely less on purposive behaviour in the locational sense, such as those in space syntax [19], become more relevant. These models do not simulate trip makers being attracted to destinations that take travel cost into account but incorporate physical characteristics of crowds which avoid obstacles of various sorts producing flocking and related behaviours, while being grounded in cognitive perception. For example, many of the papers that deal with the movement of animal populations in this special issue deal with forces of a physical kind that determine how the objects of interest move and respond to their environment. They do not, however, deal with purposive behaviour of the human variety based on decision-making that attempts to optimize socio-economic costs and benefits, but, to a large extent, all these approaches are need to complement one another.

When we scale up to cities which we represent by subdivision into small zones or neighbourhoods, sometimes called TAZs (Traffic Assignment/Analysis Zones) which often have a few thousand trip makers located within, we usually adapt these to simulate all the trips that are generated in each of these zones. We can also use the same kinds of utilities based on benefits less costs that we specified in our generic equations listed previously in (4.1) to (4.5). In fact, the model we specified in these equations is what is called singly-constrained in that the flows or trips generated sum to the activity at the origins i while the model is designed to predict activity at the destinations *j*. Formally then $O_i(t) = \sum_k O_i^k(t) = \sum_{kj} F_{ij}^k$ where we aggregate over k individuals and j destinations and $D_j(t) = \sum_k D_j^k(t) = \sum_{ki} F_{ij}^k$ where we aggregate over k individuals and i origins. We still index these flows at a cross-section in time and insofar as there is any dynamics, it is able to enter these equations through the utility terms. But as such, there are no explicit dynamic processes based on feedbacks of the kind that are key to the way the city evolves. These models are still, at best, comparative static, meaning that future states based on changing the independent variables need to be compared



Figure 3. The London ABM MATSim model at different times and different scales. The dots represent moving travellers; for the animations see https://vimeo.com/ 119354430.



Figure 4. Scaling movement models up to the national level. (a) MSOA zoning system; (b) employment density; and (c) population density.

with the existing state when this kind of 'what if' prediction is made with these models to inform the planning process.

We have built a variety of models based on equation (4.5) for different sectors in the UK space economy which we have defined from the population census geography called 'middle layer super output areas' (MSOAs). These zones contain on average around 7000 persons and there are 7201 in the model area which currently is England and Wales. The model is to be extended to Scotland shortly when the relevant data becomes available. What we show here is the journey to work model which links employment at origins $O_i(t)$ to destinations which enable us to predict the working population resident at those places as $D_i(t)$. We calibrate the model by simulating how close the predicted flows $F_{ii}^k(t)$ are to the observed $F_{ii}^{k(obs)}(t)$ estimating the individual or group specific parameters $\alpha^{k}(t)$ and $\beta^{k}(t)$ so that the average benefits and costs that the model reproduces match those of the data. The extended model simulates not only the journey to work but flows in the retail sector between population and commercial centres, as well as being extensible to include flows in the education and health sector which reflect journeys to school and to healthcare centres and hospitals.

To illustrate the model, we show the zoning system for England and Wales in figure 4a and the distribution of employment and population in figure 4b,c. These distributions are quite similar and emphasize the fact that at this scale, we see the density of cities and related settlements which is a proxy for the density of movement. The model is web-based and can be run from any location (see http:// www.quant.casa.ucl.ac.uk). In figure 5a, we show observed population again, in 5b predicted population, and in 5c the population differences as well as the observed accessibility to population from the employment sector as figure 5d. This measure of accessibility and there are many such measures which can be computed from these kinds of models, is based on potential values from the gravitational model [20], defined in this case as

$$V_{i}(t) = \sum_{jk} \exp^{\alpha^{k}(t)W_{j}^{k}(t) - \beta^{k}(t)c_{ij}^{k}(t)}$$
(5.1)

which is the competition or normalizing term from equation (4.5). $V_i(t)$ is a measure of nearness to residential population while population potential can also be computed in a



Figure 5. Observed and predicted population densities and accessibility. (a) Observed population density; (b) predicted population density; (c) differences in population density; and (d) population accessibility.



Figure 6. Average vectors computed from the journey to work flows between all 7201 origins and destinations in England and Wales. (a) Flow vectors in England and Wales; and (b) flow vectors in Greater London.

symmetric way which gives a similar measure of nearness to employment. Accessibility measures are widely applied to look at the nearness or proximity of places to one another as summations of the influence of size and distance between a place to all others and in this sense, they represent a kind of simplified movement model where movements are collapsed to location.

What is hard to visualize from these models are the flows or movements which give rise to far too messy and complex a pattern as we noted above but we can produce vectors or average flows as we did for Greater London in figure 1*f*. What we do is examine each flow $F_{ij} = \sum_k F_{ij}^k$ and consider this as a vector of length $(x_i, y_i) \rightarrow (x_j, y_j)$ of which there are F_{ij} . For each zone, we then add all these vectors to every other set of vectors and then take the average. This gives us the length and orientation of the average vector $(\Delta x_z, \Delta y_z)$ centred on *i*. This is computed as

$$\Delta x_z = \frac{\sum_j F_{ij}(x_i - x_j)}{\sum_j F_{ij}} \quad \text{and} \quad \Delta y_z = \frac{\sum_j F_{ij}(y_i - y_j)}{\sum_j F_{ij}}, \tag{5.2}$$

where the coordinates of the average vector from any point are given by $(x_i, y_i) \rightarrow (x_i + \Delta x_z, y_i + \Delta y_z)$. We show two examples of these flows for England and Wales and for Greater London in figure $6a_ib$ and this gives a fairly clear picture of the orientation and strength of movements in these regions which accords to our common perception of the density and volume of these flows.

6. Next steps: challenges in simulating aggregate movement

As we have articulated movement here, we have assumed that dynamics in general relates to the time taken from when an individual or aggregate population starts its journey at one place and finishes at some other or the same location at a later time. The dynamics that is implicit in all our models is that movement over space takes time but that it is space that is more privileged in terms of the explanatory dimension, rather than time. This is all implicit in the high-frequency city and if we wish to explore how movements change over longer time frames, we must move to thinking about the low-frequency city and the forces that drive such change. As location is a function of movement, then explanations of longer term change-how the number of journeys change more slowly reflecting changes in not when to travel but where to travel on a semi-permanent basis-involve moving to models of location and this takes us way beyond the focus of this paper to questions about the evolution of cities [7].

There are, of course, other outstanding problems involving the kinds of movements we have described here. A key problem is how different kinds of movements dovetail and integrate with one another. It is difficult to track multimodal journeys because of limits on data-for example our Oyster card data for the London Underground is much richer than the same data for public bus because individuals only need to tap in on a bus whereas they tap in and out on the subway. This makes integrating rail and bus data problematic: independent travel data is required (if available) so that such stitching can take place, and this generates probabilistic outcomes rather than absolute predictions [21]. There are theoretical problems too in linking flow systems together. For example, many individuals engage in journeys to their work but at the same time are using email and social media to communicate essential features of their job to others while sometimes working from home, sometimes working on the road and so on. To get a good perspective on cities working as flow systems, we need much more powerful theory to enable us to make sense of all this complexity. This is far from forthcoming despite the fact that some progress is being made [22]. There are an increasing number of related datasets that might inform the kinds of movements that we have focused upon here, particularly those pertaining to mobile telephone calls. One of the best examples of such work is that generated at the Senseable Cities Lab where a variety of telecoms data has been simulated and visualized to show key hotspots in cities [23] but this is a very active focus in research on the kinds of patterns explored in this paper, and substantial progress for enriching our understanding of mobility in cities is likely to come from such developments in the next decade [24].

The link between flows and networks is still problematic, particularly in the examples shown in this paper that represent flows as desires on the part of a population. These flows tend to be quasi-independent of the network system itself. In short, network science has tended to proceed quite independently of models of flow systems. Moreover, the relationships between the physical aspects of networks and the behavioural requirements and motivations of those travelling are not well worked out. Individuals moving, say, from the suburbs to the central city have many possible routes to choose from and may choose those based on the interaction of somewhat idiosyncratic factors in comparison with the more straightforward demands of getting from one location to another. This intersection of the physical with the social and economic is an age-old problem in thinking about cities but in many respects, it is likely to be somewhat more tractable from others we have raised. In progressing these issues, visualization is ever more important, and considerable progress needs to be made in visualizing such patterns in space-time as well as in broaching the question of how different spatial and temporal scales can be simultaneously visualized to provide a much more integrated understanding of movement patterns in cities [25]. These then represent directions for future work, and the interdisciplinary focus of the papers in this special issue help in their definition.

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The impact of the 'open' workspace on human collaboration

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Organizations' pursuit of increased workplace collaboration has led managers to transform traditional office spaces into 'open', transparency-enhancing architectures with fewer walls, doors and other spatial boundaries, yet there is scant direct empirical research on how human interaction patterns change as a result of these architectural changes. In two intervention-based field studies of corporate headquarters transitioning to more open office spaces, we empirically examined—using digital data from advanced wearable devices and from electronic communication servers-the effect of open office architectures on employees' face-to-face, email and instant messaging (IM) interaction patterns. Contrary to common belief, the volume of face-to-face interaction decreased significantly (approx. 70%) in both cases, with an associated increase in electronic interaction. In short, rather than prompting increasingly vibrant face-to-face collaboration, open architecture appeared to trigger a natural human response to socially withdraw from officemates and interact instead over email and IM. This is the first study to empirically measure both face-to-face and electronic interaction before and after the adoption of open office architecture. The results inform our understanding of the impact on human behaviour of workspaces that trend towards fewer spatial boundaries.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

Boundaries between 'us' and 'them' have long captured human interest. Yet even as social scientists continue to study the value of a vast array of boundaries [1], in an era in which the nature of work is changing [2–4], managers and organizational scholars have increasingly framed boundaries as barriers to interaction that ought to be spanned [5–8], permeated [9] or blurred [10] to increase collaboration. In the most physically salient and concrete example, 'spatial boundaries' [11] at work—such as office or cubicle walls—are being removed to create open 'unbounded' offices in order to stimulate greater collaboration and collective intelligence. Does it work?

Prior theory is divided—and empirical evidence mixed—on the effect that removing spatial boundaries has on human behaviour in the space previously within those boundaries (e.g. [12,13]). On the one hand, sociological theory presents a strong argument that removing spatial boundaries to bring more people into contact should *increase* collaboration and collective intelligence. The notion that propinquity, or proximity, predicts social interaction [14]—driving the formation of social ties and therefore information exchange and collaboration—is one of the most robust findings in sociology [15,16]. It has been observed in contexts as diverse as the US Congress [17,18], nineteenth-century boarding houses [19], college dormitories [14], laboratories [20], co-working spaces [21] and corporate buildings [22]. When spatial boundaries—such as walls—are removed, individuals feel more physically proximate, which, such theory suggests, should lead to more interaction. Such interaction is a necessary

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foundation for collective intelligence—a form of distributed intelligence that arises from the social interaction of individuals [23] and that predicts, more so than the intelligence of individual members, a group's general ability to perform a wide variety of tasks [24–26]. Much like the swarm intelligence observed among cognitively simple agents such as social insects and other animals [27–29], collective intelligence for groups of humans requires interaction [30]. If greater propinquity drives greater interaction, it should generate greater collaboration and collective intelligence.

On the other hand, some organizational scholars, especially social psychologists and environmental psychologists, have shown that removing spatial boundaries can decrease collaboration and collective intelligence. Spatial boundaries have long served a functional role at multiple levels of analysis, helping people make sense of their environment by modularizing it [31], clarifying who is watching and who is not, who has information and who does not, who belongs and who does not, who controls what and who does not, to whom one answers and to whom one does not [32]. This school of thought, like theories of organizational design and architecture [29], assumes that spatial boundaries built into workspace architecture support collaboration and collective intelligence by mitigating the effects of the cognitive constraints of the human beings working within them. Like social insects which swarm within functionallydetermined zones 'partitioned' by spatial boundaries (e.g. hives, nests or schools) [29], human beings-despite their greater cognitive abilities-may also require boundaries to constrain their interactions, thereby reducing the potential for overload, distraction, bias, myopia and other symptoms of bounded rationality. Research as far back as the foundational Hawthorne Studies [33,34] shows that being walled off can therefore increase interaction within the separated group [33]. Similarly, subsequent workplace design research (for reviews, see [35-38])-though mixed in its findingssuggests that open offices can reduce certain conditions conducive to collaboration and collective intelligence, including employee satisfaction [39,40], focus [41-44], psychological privacy [45,46] and other affective and behavioural responses [40,41,43,47,48]. Such negative psychological effects of open offices conceivably may lead to less, not more, interaction between those within them [49], reducing collaboration and collective intelligence.

To our knowledge, no prior study has directly measured the effect on *actual interaction* that results from removing spatial boundaries to create an open office environment. Past workplace design research, rather than directly and objectively measuring behaviours, has relied heavily on survey-based or activity-log methodologies, which provided self-reported measures, or on social observation studies, which provided an observer's subjective interpretation of human interactions. Several decades ago, when much of the workplace design research was conducted, measuring actual interaction patterns of individuals at work in both traditional and open office environments would have been prohibitively difficult, but new 'people analytics' technology has made it quite feasible.

Using two field studies of organizations transforming their office architecture by removing spatial boundaries to become more open, we empirically measure the effect on interaction, carefully tracking face-to-face (F2F) interaction before and after the transition with wearable sociometric devices [50,51] that avoid the imprecise and subjective survey-based self-reported measures typical of previous office collaboration studies [52,53]. We also measure two digital channels of interaction—email and instant messaging (IM) [54–56]—using information from the organizations' own servers.

In the first study, we focus on the most basic set of empirical questions: what is the effect of transitioning from cubicles to open workspaces on the overall *volume* and *type* of interaction, with what implications for organizational performance based on the company's own performance management system? In the second study, we replicate the first study's results and then consider two more-targeted empirical questions: how does spatial *distance* between workstations moderate the effect of transitioning from cubicles to open workspaces and how do individual employee interaction *networks*, both F2F and electronic, change differentially? While the first study considers interactions involving *individuals*, the second considers interactions for *dyads* (both sides of the interaction), allowing a more precise but limited investigation of the effects.

2. Study 1

The first empirical study, a quasi-field experiment [57,58], was conducted at the global headquarters of OpenCo1,¹ a Fortune 500 multinational. In a so-called war on walls, OpenCo1 decided to use the latest open office workstation products to completely transform the wall-bounded workspaces in its headquarters so that one entire floor was open, transparent and boundaryless.

The redesign—which required people to move from assigned seats on their original floor to similarly assigned seats on a redesigned floor of the same size—affected employees in functions including technology, sales and pricing, human resources (HR), finance, and product development, as well as the top leadership. Of those people, a cluster of 52 (roughly 40%) agreed to participate in the experiment. A comparison of HR data for participants and nonparticipants provided no evidence of nonresponse bias. Because of the nature of office space, all employees moved from the old space to the redesigned space at the same time, so the experiment was structured with an interrupted time-series design [58].

To capture a full, data-rich picture of interaction patterns both before and after the boundaries were removed, participants were asked to wear a sensor, known as a sociometric badge [59], that recorded, in great detail, their F2F interactions: an infrared (IR) sensor captured whom they were facing (by making contact with the other person's IR sensor), microphones captured whether they were talking or listening (but not what was said), an accelerometer captured body movement and posture, and a Bluetooth sensor captured spatial location (figure 1). All sensors recorded time-stamped data in 10 ms intervals. Based on prior research using these sociometric badges [50], an F2F interaction was recorded when three conditions were met: two or more badges (i) were facing each other (with uninterrupted infrared line-of-sight), (ii) detected alternating speaking, and (iii) were within 10 m of each other. The interaction ended when any of the three criteria ceased to be true for more than 5 s. While these criteria were based on precedent from significant prior use of sociometric badges, sensitivity analysis showed the results to be robust to reasonable alternative assumptions (including shorter distances in 1 m increments,



Figure 1. Sociometric badge. (Online version in colour.)

different lag times before concluding an interaction, and different speaking patterns). This F2F data was combined with email and IM data for the same time periods, collected from the company's servers, to create a full picture of these professionals' interactions before and after the redesign.

Data were collected in two phases: for 15 workdays (three weeks) before the redesign and, roughly three months later, for 15 workdays after the redesign. Three-week data collection windows were chosen as a balance between the organization's desire to minimize the burden of the research study on its employees and our need to control for the possibility of idiosyncratic daily and weekly variations in employee schedules. The three-month gap between phases was chosen for two reasons. First, work at OpenCo1's global head-quarters followed quarterly cycles, so a three-month gap allowed us to conduct the two data-collection phases at the same point in the quarter. Second, it allowed just over two months of adjustment after the move, enough for people to have settled into their new environment but not so much that the work they did could have changed much.

The dataset included 96 778 F2F interactions, 84 026 emails (18 748 sent, 55 012 received, 9755 received by cc and 511 received by bcc) and 25 691 IMs (consisting of 221 426 words). The most straightforward and conservative empirical strategy for analysing the intervention was to simply aggregate and then compare pre-intervention and post-intervention volumes:

$$Y_{it} = \alpha + (\beta_1 \times \text{Post}_{it}) + \sum \text{ person fixed effects} + \varepsilon_{it}.$$
 (2.1)

 Y_{it} the dependent variable, is the amount of interaction—F2F or electronic—where 'i' is the individual in question and 't' is the phase (pre- or post-redesign). Post_{it} is an indicator variable that equals 1 if the interaction occurred after the redesign. The main estimation used ordinary least-squares (OLS) regressions with person fixed effects, although all results were robust to the exclusion of person fixed effects. Standard errors were corrected for autocorrelation and clustered by individual [60]. If the redesign increased F2F interaction, we should see a positive and significant β_1 — the coefficient reported in the 'Post' column of table 1—when Y_{it} is F2F interaction (the first row of table 1). More generally, in table 1, the effect on a particular

kind of interaction due to the transition to more open architecture is reported in the 'post' column, where a negative number indicates reduced interaction and a positive number indicates increased interaction.

(a) Study 1 results

(i) Volume of interaction

Although OpenCo1's primary purpose in opening up the space had been to increase F2F interactions, the 52 participants now spent 72% *less* time interacting F2F. Prior to the redesign, they accumulated 5266 min of interaction over 15 days, or roughly 5.8 h of F2F interaction per person per day. After the redesign, those same people accumulated only 1492 min of interaction over 15 days, or roughly 1.7 h per person per day.

Even though everyone on the floor could see everyone else all the time (or perhaps *because* they could), virtual interaction replaced F2F interaction in the newly boundaryless space. After the redesign, participants collectively sent 56% (66) more emails to other participants over 15 days, received 20% (78) more emails from other participants, and were cc'd on 41% (27) more emails from other participants. (For the received and cc'd volumes, emails sent are counted once for each recipient.) Bcc: activity, which was low in volume and limited to a small subset of individuals, did not significantly change. IM message activity increased by 67% (99 more messages) and words sent by IM increased by 75% (850 more words). Thus—to restate more precisely—in boundaryless space, electronic interaction replaced F2F interaction.

(ii) Performance outcome

Should we be concerned about these effects? One indication of the meaningfulness of this shift in behaviour was its effect on performance. In an internal and confidential management review, OpenCo1 executives reported to us qualitatively that productivity, as defined by the metrics used by their internal performance management system, had declined after the redesign to eliminate spatial boundaries. Consistent with research on the impact of a decline in media richness on productivity [54,55] and on the particular challenges of email [61], it is not necessarily surprising that productivity declined due to a substitution of email for F2F interaction. What is surprising is that more open, transparent architecture prompted such a substitution.

3. Study 2

Given the findings from Study 1, another organization was recruited to further this research. Our goal was to conduct a conceptual replication of the first study with a longer time window. This second empirical study was also a quasi-field experiment at a Fortune 500 multinational and was conducted at the global headquarters of OpenCo2.² At the time of the study, OpenCo2 was in the process of a multi-year headquarters redesign, which—as in Study 1—involved a transformation from assigned seats in cubicles to similarly assigned seats in an open office design, with large rooms of desks and monitors and no dividers between people's desks.

We again collected F2F data using sociometric badges and email data from company servers, this time for 100 employees from a single floor, which was roughly 45% of the employees on that floor. As in Study 1, data were

4

Table 1. Impact of open offices on interaction at OpenCo1. Models are OLS with person fixed effects and with standard errors clustered by individual in parentheses. Coefficients represent minutes of face-to-face (F2F) interaction, number of email messages or IM messages, or number of words in IM between a member of the study and all others at work during the period of the study. *p < 0.05; **p < 0.01; ***p < 0.001.

type of interaction	post	constant	obs.
volume:			
F2F interaction	— 3774*	5266***	104
minutes of F2F interaction time (indicated by proximity of individuals	(1607)	(1136)	
combined with spoken words by at least one party)			
email interaction (sent)	66***	118***	104
total number of emails sent by participants to other participants	(19)	(13)	
email interaction (received: To)	78***	394***	104
total number of emails received by participants from other participants, where	(21)	(15)	
the recipient appeared in the 'To:' field			
email interaction (received: cc)	27***	66***	104
total number of emails received by participants from other participants, where	(8)	(6)	
the recipient appeared in the 'Cc.' field			
email interaction (received: bcc)	-1	6***	104
total number of emails received by participants from other participants, where	(1)	(1)	
the recipient appeared in the 'Bcc:' field			
IM interaction (number of messages)	99**	147***	104
total number of instant messages sent by participants to other participants	(30)	(21)	
IM interaction (cumulative word count of messages)	850***	1140***	104
total number of words sent in instant messages by participants to other participants	(218)	(154)	

collected in two phases: for eight weeks starting three months prior to the redesign of this particular floor and for eight weeks starting two months after the redesign. But for this study, we also collected detailed data on the participants; namely, three employee attributes-gender, team assignment and role-and one architectural attribute-desk location. In the first phase, desks were in cubicles, so seats were roughly 2 m apart and directly adjacent to one another. In the second phase, seats still lay roughly 2 m apart and directly adjacent to one another, but were grouped at undivided and unwalled tables of six to eight. Seat location allowed us to calculate the physical distance between dyads of employee workstations before and after the redesign, such that we could include physical distance, as well as the other employee attributes, as control variables. The OpenCo2 dataset included 63 363 min of F2F interaction and 25553 emails, all generated by 1830 dyads-those with interaction-of the 100 employees involved. Mindful of Study 1's consistent results across multiple forms of electronic communication, Study 2 only collected email data to measure electronic interaction. The empirical strategy was similar:

$$Y_{jt} = \alpha + (\beta_1 \times \text{Post}_{jt}) + \sum \text{dyad fixed effects} + \varepsilon_{jt}$$
 (3.1)

and

$$Y_{jt} = \alpha + (\beta_1 \times \text{Post}_{jt}) + (\beta_2 \times \text{Physical Distance}_{jt}) + (\beta_3 \times \text{Gender}_j) + (\beta_4 \times \text{Team}_j) + (\beta_5 \times \text{Role}_j) + \varepsilon_{jt}.$$
 (3.2)

In equation (3.1), as in equation (2.1), Y_{jt} , the dependent variable, is the amount of interaction, F2F or electronic. However, because the physical-distance control variable was dyadic, Y_{jt} must also be specific to a particular dyad 'j' (rather than to an individual 'i', as in Study 1). As in Study 1, 't' refers to the phase (pre- or post-redesign). Post_{it} is an indicator variable that equals 1 if the dyadic interaction occurred after the redesign. In equation (3.2), we investigate specific control variables-characteristics of each dyadrather than just dyad fixed effects. Physical Distance_{it} is the distance between the dyad's workstations, measured as the shortest walking path (in metres). Gender_i, Team_i and Role_i are indicator variables that equal 1 if the two individuals in the dyad were of the same gender, on the same team, or in the same role, and equal 0 otherwise. The main estimation used OLS regressions with either dyad fixed effects (2) or distance, gender, team and role controls (3). Standard errors of the coefficients were corrected for autocorrelation and clustered by dyad [60]. If the redesign increased F2F interaction, we should see a positive and significant β_1 —the coefficient reported in the 'post' row of table 2-when Yit is F2F interaction. More generally, in table 2, we report the effect of the transition to open architecture on particular types of interaction in the 'post' row, where a negative number indicates reduced interaction and a positive number indicates increased interaction. For the control variables, we report the coefficient for the entire sample without regard to whether the office architecture involved cubicles or open spaces, as our purpose in including those variables is to remove gender, team and role effects from the variable of interest, Post. For example, the significant and positive coefficient for Team means that those on the same team communicated more than those on different teams (for both cubicles and open spaces), and the significant and positive coefficient for Role means that those in the same role communicated more than those in different roles (for both cubicles and open spaces).

Table 2. Impact of open offices on interaction at OpenCo2. Models are OLS with standard errors clustered by dyad in parentheses. Models 1 and 3 include dyad fixed effects. In Models 1 and 2, coefficients represent minutes of F2F interaction between a particular dyad during the period of the study. In Models 3 and 4, coefficients represent number of emails between a particular dyad during the period of the study. *p < 0.05, **p < 0.01, ***p < 0.001.

	1	2	3	4
type of interaction	F2F with fixed effects	F2F with controls	email with fixed effects	email with controls
change in volume:				
post	— 12.79***	-9.81***	1.24***	1.54***
0 if before redesign, 1 if after	(1.39)	(1.27)	(0.31)	(0.32)
physical distance	-0.01	-0.07***	-0.00	-0.01
walking distance (in metres) between desks	(0.02)	(0.02)	(0.01)	(0.01)
gender		2.08		0.08
0 if different genders, 1 if same		(1.37)		(1.02)
team		41.02***		33.86***
0 if different teams, 1 if same		(2.53)		(1.80)
role		9.59***		3.12*
0 if different roles, 1 if same		(1.91)		(1.42)
constant	17.99***	14.63***	5.75***	3.07***
	(1.27)	(1.47)	(0.28)	(0.85)
observations	3660	3660	3660	3660

(a) Study 2 results

(i) Volume of interactions

As a result of the redesign, 643 dyads decreased their F2F interaction and 141 dyads increased it. At the same time, 222 dyads decreased their email interaction and 374 dyads increased it. Like OpenCo1, OpenCo2 had hoped, by opening up the space, to increase F2F interactions, but the results did not bear this out. The 100 employees—or 1830 dyads—we tracked spent between 67% (Model 1, 12.79/17.99) and 71% (Model 2, 9.81/14.63) *less* time interacting F2F. Instead, they emailed each other between 22% (Model 3, 1.24/5.75) and 50% (Model 4, 1.54/3.07) more.

As one might suspect, dyads on the same team or with the same role communicated more, both F2F and by email, relative to dyads on different teams or in different roles. Gender, in contrast, had no significant effect on the volume of either form of interaction. Physical distance did show a small inverse effect on F2F interaction (Model 2): the nearer the two workstations, the more F2F interaction. This effect was notable both for its small size relative to the size of the effect of the open office and for the fact that it was limited to F2F interaction (not email). We investigate this in further detail next.

(ii) The effect of physical distance on F2F versus email

Model 2 of table 2 shows that the effect of physical distance on F2F interaction is small—and the effect on email insignificant—relative to that of openness. The relatively small effect of distance on F2F interaction was surprising given that repeated studies have shown that people talk more to those who are physically closer to them [62,63]. When others are physically proximate, it is easier to be aware of them [64], start conversations with them [64,65], unexpectedly encounter or overhear them [66], and manage their impressions of our collaborative work behaviour [67]. Nonetheless, our review of these prior

studies found none that directly measured interaction volumes, and thus perhaps—while present—the effect of distance on F2F interaction may be far more minimal than previously thought.

Table 2, however, does not allow us to compare the relative effects of physical distance on F2F interaction and on email interaction. To do so, we used a latent space model called the Latent Position Clustering Model [68] to take into account clustering and to control for other covariates. We find that physical distance affected F2F interaction twice as much as it did email interaction. As a robustness check, we used several machine learning algorithms, such as a Random Forest, to see if changes in F2F networks prompted by changes in physical distance predicted changes in email networks. Across all models, we find that F2F networks and email networks respond very differently to changes in the built environment, with changes in one type of network failing to predict changes in the other.

This variance between the adaptation of F2F and electronic networks in response to a change in physical space is an important finding for future research on collaboration and collective intelligence. In several notable cases, past research has relied on email alone [69,70] to study topics ranging from the Enron debacle to the relationship between office layout and interaction, basing claims about F2F interaction on findings from electronic interaction data. Our finding that changes in workplace design affect electronic and F2F interaction networks differently (and, on some measures, in opposite directions) should make future researchers wary of using one network as a proxy for the other.

4. Discussion

We began with a specific research question: does removing spatial boundaries at work to create open, unbounded offices

increase interaction? Our two empirical field studies were consistent in their answer: open, unbounded offices reduce F2F interaction with a magnitude, in these contexts, of about 70%. Electronic interaction takes up at least some of the slack, increasing by roughly 20% to 50% (as measured by 'To:' received email).

Many organizations, like our two field sites, transform their office architectures into open spaces with the intention of creating more F2F interaction and thus a more vibrant work environment. What they often get—as captured by a steady stream of news articles professing the death of the open office [71–73]—is an open expanse of proximal employees choosing to isolate themselves as best they can (e.g. by wearing large headphones [74]) while appearing to be as busy as possible (since everyone can see them). Recent studies [75] and earlier research [40,41,43,47,48] have investigated the self-reported dissatisfaction of employees in open offices, but to our knowledge, we are the first to empirically study the direct behavioural impact of open office space on the volume of F2F and electronic interaction. Our results support three cautionary tales.

First, transitions to open office architecture do not necessarily promote open interaction. Consistent with the fundamental human desire for privacy [76] and prior evidence that privacy may increase productivity [32,45], when office architecture makes everyone more observable or 'transparent', it can dampen F2F interaction, as employees find other strategies to preserve their privacy; for example, by choosing a different channel through which to communicate [39]. Rather than have an F2F interaction in front of a large audience of peers, an employee might look around, see that a particular person is at his or her desk, and send an email.

The second caution relates to the impact of a transition to open office architecture on collective intelligence. We still have much to learn about how collective intelligence works [77], as we borrow from and distinguish parallel work on swarm intelligence among social insects and some other animals. While the earliest work assumed open spaces would promote collective intelligence among humans, our findings support more recent work that has begun to suggest otherwise. Kao & Couzin, in modelling the presence of multiple cues and the possibility of observing them, find that intermediate (rather than maximal) levels of cues produce higher levels of collective intelligence [78]. We see a close relationship between our finding that open, 'transparent' offices may be overstimulating and thus decrease organizational productivity and Kao & Couzin's demonstration that finitely bounded, and often small, group size maximizes decision accuracy in complex, realistic environments. Similarly, recent collective intelligence work suggests that, like our open offices, too much information from social data can be problematic, partly because of challenges focusing attention [74,79], but also for reasons that extend to more general functions of human cognition. For example, by connecting human cognition and collective intelligence with the behaviour of eusocial insects, Toyokawa et al. found that richness in social information was detrimental to collective intelligence outcomes, with performance being best when social learning opportunities were constrained [80]. Similarly, in a study involving human subjects, Bernstein et al. found that intermittent rather than constant social influence produced the best performance among humans collectively engaged in complex problem solving [81]. As we are reminded in Hight & Perry's article on collective intelligence and architectural design, 'collective intelligence is not simply technical, but also explicitly social, political, and by extension, professional' [2, p. 6]. Our findings empirically reinforce their caution that the relationship between architectural design and collective intelligence extends beyond technical considerations.

The third caution is that transitions to open office architecture can have different effects on different channels of interaction. In our studies, openness decreased F2F interaction with an associated increase in email interaction. In the digital age, employees can choose from multiple channels of interaction [54] and a change in office architecture may affect that choice.

Complementing prior research on media richness suggesting that substituting email for F2F interaction can lower productivity [53], our studies highlight two other consequences. First, because fundamentally different mechanisms drive F2F and email interaction, the physical propinquity that redesigned offices seek to achieve has a direct effect only on F2F interaction, not on email, yet drives interaction from F2F to email. Adopting open offices, therefore, appears to have the perverse outcome of reducing rather than increasing productive interaction. Second, F2F and email networks differ. Although prior studies have investigated one or the other [56,82], none has empirically linked F2F and email network interaction to discern how good a proxy one is for the other. We find that they are poor proxies for each other. Therefore, an intervention that redirects interaction from one network to another, like the open office redesigns studied here, not only changes the channel of interaction, but also skews whom a person interacts with. That can have profound consequences for how-and how productively-work gets done.

In summary, because the antecedents of human interaction at work go beyond proximity and visibility, the effects of open office architecture on collaboration are not as simple as previously thought. While it is possible to bring chemical substances together under specific conditions of temperature and pressure to form the desired compound, more factors seem to be at work in achieving a similar effect with humans. Until we understand those factors, we may be surprised to find a reduction in F2F collaboration at work even as we architect transparent, open spaces intended to increase it.

Data accessibility. We are unable to provide open access to our data owing to their sensitive nature and the nondisclosure and confidentiality agreements that surround them. Please contact the corresponding author for more information.

Authors' contributions. E.S.B. carried out all work on Study 1 and drafted the manuscript. S.T. carried out all work on Study 2 and helped draft the manuscript. Both authors gave final approval for publication. Competing interests. We declare we have no competing interests.

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Endnotes

¹OpenCo1 is a pseudonym for the corporation's real name, which has been anonymized.

²OpenCo2 is a pseudonym for the corporation's real name, which has been anonymized.

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8

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Predicting collective behaviour at the Hajj: place, space and the process of cooperation

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Around 2 million pilgrims attend the annual Hajj to Mecca and the holy places, which are subject to dense crowding. Both architecture and psychology can be part of disaster risk reduction in relation to crowding, since both can affect the nature of collective behaviour-particularly cooperationamong pilgrims. To date, collective behaviour at the Hajj has not been systematically investigated from a psychological perspective. We examined determinants of cooperation in the Grand Mosque and plaza during the pilgrimage. A questionnaire survey of 1194 pilgrims found that the Mosque was perceived by pilgrims as one of the most crowded ritual locations. Being in the plaza (compared with the Mosque) predicted the extent of cooperation, though crowd density did not. Shared social identity with the crowd explained more of the variance than both location and density. We examined some of the process underlying cooperation. The link between shared social identity and giving support to others was stronger in the plaza than in the Mosque, and suggests the role of place and space in modulating processes of cooperation in crowds. These findings have implications for disaster risk reduction and for applications such as computer simulations of crowds in pilgrimage locations.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

The Hajj has been called the world's 'global gathering' because people from all over the world attend this annual Muslim pilgrimage to the holy places in and around Mecca [1]. Taking part in the Hajj is expected of all able-bodied and financially capable Muslims at least once in their lifetime. It involves participating in rituals at specified spiritual locations during a certain 5-day period.¹ These requirements, combined with the ease of modern air travel, mean that millions of people attend the Hajj—1 862 909 was the official figure (not counting unofficial pilgrims) in 2016, for example [2]. Therefore, the holy places are very crowded during Hajj. Overcrowding has been linked to fatalities at the Hajj in the past. In 2006 for example, 346 pilgrims died in a crowd crush at the entrance to Jamaraat Bridge [3], and at least 717 died in a crush at Mina in 2015 [4].

Architecture has been seen as part of the solution to this source of risk. The Jamaraat structure was redesigned following the 2006 disaster to allow pilgrims to 'stone the devil' on three different floors, increasing capacity [5]. Research in psychology suggests that collective behaviour is also important in disaster risk reduction [6,7]. Indeed, architecture and psychological processes can interact to produce forms of collective behaviour that reduce, or contribute to, risk. For example, in emergency evacuations a combination of a narrow exit and unfamiliarity with layout are among the predictors of dangerous pushing and trampling [8].



Figure 1. Crowd close to the black stone, at the Ka'aba (picture courtesy of Wessam Hassanin).



Figure 2. Al-Masjid Al-Haram, or Grand Mosque, Mecca, with the Ka'aba at centre and pillars round edge.

Cooperation is a crucial form of collective behaviour at the Hajj, in two ways. First, harmonious relations with others are a spiritual value which is both salient and expected at the Hajj, alongside related values such as unity and peacefulness [9]. Second, cooperation is also a practical necessity. This is particularly the case in the Grand Mosque and other very crowded locations, where failure to coordinate with others—for example pushing, not allowing others space could lead to a crowd collapse and fatalities.

At the time of the 2012 Hajj (the focus of the present study), the Al-Masjid Al-Haram (or Grand Mosque) covered an area of 356 800 m² (88.2 acres) [10]. The Mosque contains the *Ka'aba*, a small black cube-shaped building that is the holiest site on Earth to Muslims, since it is said to have been built by Abraham [11]. When Muslims pray, wherever they are in the world, they turn in the direction of the Ka'aba (this is known as *qibla*). On visits to Mecca, pilgrims circumambulate the Ka'aba seven times (*tawaf*). During Hajj, they also attend the Mosque for daily prayer, facing the Ka'aba.

The experience of seeing the Ka'aba is emotionally intense for pilgrims [12]. The communal nature of the experience is emphasized by the fact that all the pilgrims wear a simple white robe for the majority of the rituals; this serves to convey unity, equality and universality in the shared submission to God. But as well as joy and harmonious behaviour, there is also competitive behaviour within the Mosque, as people strive to get close to the Ka'aba, particularly near the black stone, and some use physical force to do so (figure 1). Some enter the Mosque only to find their view of the Ka'aba obscured by pillars (figure 2). Instead, many pilgrims carry out their prayers on the plaza immediately outside (figure 3), where the emotional experience may be less intense, but also less variable, since expectations and competition are both lower.

Despite the importance of understanding collective behaviour at the Hajj, there has been almost no research on this topic. Understandably, most studies of the Hajj examine the public health issue of disease (e.g. [13]). Where collective behaviour is referred to, it tends to be only as a 'panic' or 'stampede' [14], despite the vast majority of Hajj rituals passing without incident.

The emphasis on negative collective behaviour in previous research on the Hajj reflects the history of crowd psychology, which has been overly preoccupied with crowd violence [15,16]. Classical crowd psychology claimed that becoming 'submerged' in a crowd leads to a diminution of self; in this reduced psychological state, primitive aggressive drives, grounded in a 'racial unconscious' [17] or individual biology [18], would predominate, leading to uncontrolled violence. One problem for this approach is that most crowd


Figure 3. Plaza outside the Grand Mosque.

events are peaceful. The approach notably fails to explain behaviour at ritual and ceremonial crowd events, where the act of coming together *reinforces* values and norms, rather than leading people to abandon them [19,20].

The Hajj is an example of such a ritual crowd, and the present study is part of a wider project to examine the psychological and contextual basis of positive experiences and behaviour in crowds, based on the social identity approach [21]. The social identity approach suggests that self or identity is composed of categorizations of self and other that vary in inclusivity in different social contexts [22,23]. The approach has been applied to standard topics in social, organizational and health psychology [24,25]. It has also been used to understand the psychology of place and space across a range of crowd events. Thus a multimethod study of an overcrowded music festival found that the lack of space was uncomfortable only for those who did not share social identity with the rest of the crowd [7]. An interview study of an Orange Order parade in Northern Ireland indicated that domination of the soundscape was a way of imposing identity on the streets [26]. Research on urban riots has repeatedly shown that many of the actions of rioters against police and property reflect a common identity defined in terms of home location and a desire to eject police from that shared territory [27,28].

The social identity approach agrees with early classical crowd psychology that emotion is a central feature of the phenomenology of many crowd events [21]. However, rather than seeing emotion as primitive and irrational, it suggests that emotional experiences are grounded in our knowledge of our group memberships and in the relationships we have with others in our group [19]. In short, collective behaviour and emotional experience is a function not of a loss of self but of a *shared* self.

The aim of the present study was to explore some of the determinants of cooperation in the Grand Mosque and plaza during Hajj, in order to contribute to an understanding of how collective behaviour operates in these locations. By sampling a relatively matched sample of pilgrims inside and outside the Mosque, we were able to analyse the possible roles of location and crowd density in cooperative behaviour in these locations. We also sought to examine the role of shared social identity in such cooperative behaviour. Shared social identity [21] is the subjective perception that others are in the same social group as oneself, and indeed share selfhood with one. Shared social identity has been shown reliably to increase bystander helping [29], practical and emotional social support in emergencies [30,31], and mundane solidarity behaviours at a (Hindu) pilgrimage [32]. In the present study, we measured shared social identity in two ways: participants' perception that others in the crowd are good Muslims (i.e. good ingroup members), and participants' identification with the crowd.

We surveyed 1194 pilgrims during the Hajj in 2012. In this paper, first we explore descriptively pilgrims' experience of crowdedness, showing that the Mosque was experienced as the most crowded ritual location. Using researchers' estimates, we then examine any differences in crowd density between the plaza and the Mosque at the time of sampling. To investigate determinants of cooperation, we examine the extent to which location (inside the Mosque or in the plaza) and crowd density each affect pilgrims' perceptions of support provided by others. To further investigate cooperation, we examine predictors of self-reported social support given. Since inside the Mosque there are enhanced expectations but also (for many people) obstructive architecture and competition for the best view of the Ka'aba, we expect that selfreported social support will be slightly lower in the Mosque than in the plaza. We also expect that shared social identity will be significantly and positively associated with giving social support. Finally, we unpack the process of cooperation using structural equation modelling. Based on the notion that others' (normative) behaviour can tell us something about their category membership [33], and that their category membership can affect our behaviour towards them [29,30], we investigated the extent to which perceiving social support in the crowd predicts shared social identity (perceiving others as good Muslims and then identification with the crowd) and shared social identity predicts giving social support. We suggest that if space and place do shape cooperation then this process will also be affected. Specifically, the reduction in social support given in the Mosque compared with the plaza will be accounted for by a reduction in the power of the main predictor, shared social identity.

With respect to the problem of disaster risk reduction at the annual Hajj, our approach suggests a view of collective

4

behaviour different to the assumption that the crowd is simply a problem that planners have to work around. In this account, shared social identity in the crowd facilitates the cooperative behaviour needed in valued locations where dense crowds gather: it motivates people to be supportive, and it enables them to anticipate each other's behaviour. These processes of self-organization occur 'naturally' in many crowds, though organizers can play a role in supporting them (for example by providing information, communicating regularly, and so on). If our analysis is correct, it means there is a role for social psychology in planning for mass gatherings and crowd safety management training [7,34], when grounded in a broader understanding of place and space in relation to the built environment.

2. Methods

(a) Recruitment procedure

We surveyed 1194 pilgrims, sampling in a way stratified by the main languages of pilgrims at the Hajj: 420 (35%) were Arabic speakers, 150 (13%) were speakers of Malay, 150 (13%) of Urdu, 120 (10%) of French, 120 (10%) of Persian, 120 (10%) of Turkish and 114 (9%) of English. Twelve research assistants, native speakers of the seven languages, were trained to recruit pilgrims with verbally administered questionnaires. The research assistants were all male, but three of them were accompanied by their wives in order to facilitate recruitment of female participants. We recruited 421 (35.7%) participants inside the Grand Mosque and 753 (64.0%) on the plaza immediately outside. Recruitment took place in three phases: 383 (32.5%) participants were surveyed in the 9-day period when people arrive in Mecca; 533 (45.2%) during Hajj rituals; and 260 (22.0%) at the farewell tawaf period.² (Information on the recruitment time and location of four participants was missing.) Each questionnaire took around 38 min to complete.

(b) Measures

Density: the research assistants estimated the number of people per square metre (ppm²) around each participant they recruited.

Most subjectively crowded ritual locations. Participants were asked to rank the crowdedness of five ritual locations: sa'ee (moving between the hills of Safa and Marwa in the Grand Mosque, symbolizing Hagar's search for water for her son), tawaf, Jamaraat, standing in Muzdalifah, and Nafrah (leaving Arafat).

Cooperation was measured in two ways: first, participants' *perceptions that others give social support* (three items, e.g. 'In my view, most pilgrims are supportive of others'; $\alpha = 0.78$); and second, participants' reports of *giving social support* to others on the Hajj (two items, e.g. 'I have been helpful to others'; $\alpha = 0.66$). Responses on these items and those below (other than demographics) were assessed on a seven-point Likert scale, ranging from 'agree strongly' to 'disagree strongly'. (See electronic supplementary material for full details of these and other items.)

Perceptions that others in the crowd are good Muslims were measured with three items (e.g. 'In my view, other people in this crowd are good Muslims'; $\alpha = 0.79$). Identification with the crowd was measured with three items (e.g. 'I feel a sense of togetherness with other people on the Hajj'; $\alpha = 0.80$).

Demographic measures taken included age, gender, level of education, previous experience of the Hajj, nationality and language.

Acquiescence: to control for the possibility that some participants would agree with questionnaire items whatever the content, we created a measure of acquiescence by averaging scores of those items that pointed in two different directions. Full details are provided in the electronic supplementary material.

3. Results

The results are divided into four sections. First, we present sample characteristics. Second, we provide analysis of participants' perceptions of the most crowded locations and researchers' estimates of crowd density. Third, we examine predictors of cooperation. Finally, we present structural equation modelling of the process of cooperation across the Mosque and plaza locations.

(a) Sample characteristics

Generally, it was difficult to persuade pilgrims to take part in the study, especially close to the Ka'aba, since they were there to worship rather than to fill in a questionnaire. Response rates were around 60% inside the Mosque and around 70% on the plaza. There were also some demographic factors noted. Thus response rates were found to decline with increasing age. Some pilgrims declined to participate on the grounds that they were illiterate (and sometimes passed us to a relative instead). Finally, women were more likely to refuse than were men.³

The data for 18 participants were entered incorrectly by one research assistant. As there was no way subsequently of correcting these, the data from these participants were removed from the analysis. Inspection of the density data revealed that seven participants were scored at 0 ppm² and three were scored at implausibly high density (12 ppm² and 15 ppm²). The data from these participants were also removed, leaving 1166 participants in the final dataset.

Seven hundred and fifty-two (64.5%) of the participants were male and 414 (35.5%) were female. This matches the proportion of males to females in the population attending Hajj in 2012 [35]. Seventeen participants (1.5%) were aged between 18 and 19 years old; 97 (8.3%) were aged 20 to 29; 223 (19.1%) were aged 30 to 39; 452 (38.8%) were aged 40 to 49, and 377 (32.3%) were aged 50 years and over. Sixty-six participants (5.7%) were illiterate, 193 (16.6%) were educated to 'read and write' level, 193 (16.6%) to primary school level, 236 (20.2%) to secondary school level, 393 (33.7%) to undergraduate degree level, 77 (6.6%) had Master's degrees, and 8 (0.7%) had doctorates. Three hundred and sixty-seven (31.2%) participants had been on Hajj before, whereas for 799 (68.5%) this was their first time.

The study included participants from 72 countries. The majority of pilgrims attend through arrangement with the six Hajj travel establishments, or travel agencies, which are (mostly) structured by geographical region. In most cases, the proportion in our sample from each establishment roughly corresponded with official estimates [35] for the event as a whole: Arab and Arabian Gulf countries 36.1%; America, Australia and Europe (including Turkey) 18.8%; South Asia 13.8%; South East Asia 11.7%; Iran and Tajikistan 10.4%; and non-Arab African Countries 9.2%.

(i) Sample characteristics: Mosque versus plaza

The sample from the plaza (n = 753) was larger than that from inside the Mosque (n = 418). For age and level of education the numbers sampled in each location were proportionate to these numbers, but there were significant differences for the other variables. For gender, men made up 64% of the overall sample but the proportion of men compared with women sampled within the Mosque was 59%. Pilgrims for whom **Table 1.** Perceived crowdedness of ritual locations (means (M) and standard deviations). M = 5, most crowded; M = 1, least crowded.

location	М	s.d.
tawaf	3.98	1.38
sa'ee	2.45	1.12
Nafrah	3.04	1.29
Jamaraat	2.91	1.40
Muzdalifah	2.62	1.28

this was their first Hajj made up 69% of the overall sample, but the proportion of these new people who were sampled within the Mosque was 74%. In the sample as a whole, the proportion of non-Arab African country pilgrims was 9%, but this group made up 18% of those sampled in the Mosque. In the sample as a whole, the percentage of French speakers was 9%, but the percentage of French speakers sampled inside the Mosque was 22%. (Statistics for these tests can be found in the electronic supplementary material.)

(b) Crowdedness and density by Hajj location

For participants' ranking of the crowdedness of the five ritual locations, a repeated measures ANOVA with pairwise comparisons showed that participants evaluated tawaf as significantly more crowded than each of sa'ee (p < 0.001), Nafrah (Arafat, p < 0.001), Jamaraat (i.e. stoning the devil, p < 0.001), and standing in Muzdalifah (p < 0.001)—see table 1 for means and s.d. When we compared researchers' density estimates for participants surveyed inside the Grand Mosque (mean (M) = 5.63 ppm², s.d. = 1.47) with those surveyed in the plaza (M = 4.96 ppm², s.d. = 1.85) using regression, as expected location significantly predicted estimated density, b = -0.185, p < 0.001. These results are in line with the expectation that the Mosque itself would be especially crowded.

(c) Predictors of cooperation

Descriptives and correlations for all measures are presented in table 2. The first examination of predictors of cooperation used perceived social support in the crowd as the dependent measure. As table 3 shows, in the first block of the regression equation, four of the control variables were significant predictors. Participants in the 40-49 age bracket reported most, and those under 20 reported least, perceived social support. French speakers, those from Turkey, America, Australia and Europe, and those from non-Arab African countries were less likely than others to perceive social support whereas those high in acquiescence were more likely to report perceiving social support. (See electronic supplementary material for additional statistics.) The second block comprised the two 'place and space' variables: density and location, neither of which was a significant predictor. The R^2 change from block 1 to block 2 was not significant, p = 0.14.

The second examination of predictors of cooperation used the measure of the participant *giving social support* to others. Table 4 shows that four of the control variables were predictive. Older participants were more likely to report giving social support than were younger participants. Male participants were more likely to report giving social support than were female participants. Higher level of education predicted more support given. French speakers gave less support than the other language groups. Those who had been to Hajj before gave more support than those for whom it was the first time. (See electronic supplementary material for additional statistics.) When the 'place and space' variables were added in block 2, density was not predictive, but location was: more social support was given in the plaza than in the Mosque (though levels of social support given were high in both locations): $M_{Mosque} = 5.89$, s.d. = 0.85; $M_{plaza} = 6.19$, s.d. = 0.84). The R^2 change from block 1 to block 2 was significant, p = 0.044. When the shared social identity variables were then added in a third block, perception that others were good Muslims and identification with the crowd each positively predicted giving support (table 4). Importantly, the final block explained considerably more of the variance than the other two, and the R^2 change from block 2 to block 3 was significant, p < 0.001.

(d) The process of cooperation

We used R to conduct structural equation modelling (SEM) with robust maximum likelihood on the direct and indirect pathways from perceived social support to giving social support via the perception that others are good Muslims and then identification with the crowd—see figure 4. We included the following variables as covariates: education, language, prior experience of the Hajj, and acquiescence.⁴

We first performed confirmatory factor analysis to explore the measurement models for all participants, and then separately for participants inside the Grand Mosque and on the plaza. The fit indices of the measurement model for participants in both locations were Akaike information criterion (AIC) = 49 147.588, root mean square error of approximation (RMSEA) = 0.072, Standardized Root Mean Square Residual (SRMR) = 0.049, confirmatory fit index (CFI) = 0.891, χ_{99}^2 = 680.691, p < 0.001; inside the Grand Mosque, AIC = 16 759.791, RMSEA = 0.060, SRMR = 0.046, CFI = 0.908, χ_{99}^2 = 242.939, p < 0.001; in the plaza, AIC = 32 050.306, RMSEA = 0.090, SRMR = 0.059, CFI = 0.851, χ_{99}^2 = 685.153, p < 0.001. Overall, the fit indices suggest that the order of the serial mediation is a good model, and conducting separate models for the two locations provides the best measurement.

When exploring the model for participants in both locations, the fit statistics were AIC = 51372.174, RMSEA = 0.071, SRMR = 0.047, CFI = 0.889, $\chi^2_{99} = 680.054$, p < 0.001. There was a significant direct effect, b = 0.391, p < 0.001, z =7.615, but the indirect effect was non-significant, b = 0.181, p = 0.063, z = 1.859. There were significant direct effects of perceived social support on the perception of others as good Muslims, b = 0.354, p < 0.001, z = 0.160, on social identification with the crowd, b = 321, p < 0.001, z = 6.220, and on giving social support, b = 0.391, p < 0.001, z = 5.327, and a significant direct effect of the perception of others as good Muslims on social identification with the crowd, b = 0.534, p < 0.001, z = 4.741. However, the direct effect of perceiving others as good Muslims on giving social support was nonsignificant, b = 0.140, p = 0.098, z = 1.657, as was the effect of social identification with the crowd on giving social support, b = 0.111, p = 0.199, z = 1.283. All indirect effects were non-significant: perceived social support on giving social support via social identification with the crowd, b = 0.035,

Table 2. Means, standard deviations and correlations. *p < 0.05; **p < 0.01.

	mean	s.d.	2	3	4	5	6
acquiescence	4.77	0.63	0.09**	0.08**	0.07*	0.02	0.15**
perceived social support	5.83	0.96		0.39**	0.30**	0.43**	0.03
giving social support	6.08	0.86			0.27**	0.33**	-0.03
others are good Muslims	6.16	0.71				0.52**	-0.06
social identification with crowd	6.05	0.78					-0.10**
estimated density	5.20	1.75					



Figure 4. Structural equation model for both locations.







total effect: b = 0.407, p < 0.001



Figure 7. Alternative model 1: inside the Grand Mosque.



Figure 8. Alternative model 1: in the plaza.



Figure 9. Alternative model 2: inside the Grand Mosque.



indirect effect: *b* = 0.165, *p* = 0.602 total effect: *b* = 0.659, *p* < 0.001

Figure 10. Alternative model 2: in the plaza.

	step 1					step 2				
	q	s.e. B	β	þ	95% CI for b	q	s.e. B	β	d	95% Cl for b
constant	4.87	0.28		< 0.001	(4.32, 5.42)	4.82	0.28		< 0.001	(4.26, 5.38)
age group	0.09	0.03	0.09	0.002	(0.03, 0.15)	0.08	0.03	0.09	0.006	(0.02, 0.14)
gender	- 0.05	0.06	-0.02	0.428	(-0.16, 0.07)	-0.06	0.06	- 0.03	0.299	(-0.18, 0.05)
education	0.02	0.02	0.03	0.425	(-0.03, 0.06)	0.02	0.02	0.03	0.398	(-0.02, 0.06)
language (French versus rest)	-0.87	0.13	-0.26	< 0.001	(-1.13, -0.61)	-0.93	0.14	-0.28	< 0.001	(-1.19, -0.66)
Hajj service (non-Arab African versus rest)	0.28	0.13	0.08	0.035	(0.02, 0.54)	0.29	0.13	0.09	0.032	(0.03, 0.55)
performed Hajj before	- 0.01	0.06	<-0.01	0.932	(-0.13, 0.12)	- 0.01	0.06	- 0.01	0.852	(-0.13, 0.11)
acquiescence	0.14	0.04	0.09	0.002	(0.05, 0.22)	0.14	0.05	0.09	0.003	(0.05, 0.23)
estimated density (persons per square metre)						0.03	0.02	0.05	0.134	(-0.01, 0.06)
Mosque versus plaza		-				-0.06	0.06	-0.03	0.306	(-0.19, 0.06)

p = 0.90, z = 1.310; perceived social support on giving social support via the perception of others as good Muslims, b = 0.050, p = 0.118, z = 1.564; perceived social support to giving social support via the perception of others as good Muslims and social identification with the crowd was non-significant, b = 0.021, p = 0.237, x = 1.183. The path model is presented in figure 4.

(i) Inside the Grand Mosque

The model fit for participants inside the Grand Mosque was AIC = 18233.213, RMSEA = 0.064, SRMR = 0.048, CFI =0.894, $\chi^2_{99} = 268.926$, p < 0.001. Most of the direct paths remained significant with the exception that the direct effect of perceiving others as good Muslims on social identification with the crowd became non-significant, b = 0.224, p = 0.108, z = 3.629, and all indirect pathways remained non-significant. Overall, the direct effect was significant, b = 0.783, p < 0.001, z = 4.697, but the indirect effect was non-significant, b = -0.188, p = 0.351, z = -0.934. The indirect path from perceived social support via perceptions that others are good Muslims to giving social support was non-significant, b = -0.038, p = 0.712, z = 0.369; the indirect path from perceived social support via identification with the crowd to giving social support was non-significant, b = -0.069, p =0.423, z = -0.801, and the indirect path from perceived social support to giving social support via the perception of others as good Muslims and social identification with the crowd was non-significant, b = -0.009, p = 0.601, z = -0.523. The path model is presented in figure 5.

(ii) On the plaza

The model fit for participants on the plaza was AIC = 32 835.680, RMSEA = 0.082, SRMR = 0.056, CFI = 0.857, χ_{99}^2 = 417.163, p < 0.001. There was a significant direct effect, b = 0.266, p < 0.001, z = 5.742, and a significant indirect effect, b = 0.311, p = 0.007, z = 2.699. The indirect effect from perceived social support to giving social support via perceptions that others are good Muslims was non-significant, b = 0.034, p = 0.241, z = 1.171, and the indirect path from perceived social support to giving social support via the perception of others as good Muslims and social identification with the crowd was nonsignificant, b = 0.039, p = 0.105, z = 1.623, but there was a significant indirect effect from perceived social support to giving social support via identification with the crowd, b = 0.067, p = 0.033, z = 2.136. The path model is presented in figure 6.⁵

Using the criteria for model fit set out by Hu & Bentler [36], where RMSEA < 0.06, SRMR < 0.08, CFI > 0.95, all models demonstrate modest fit. Based on Busemeyer & Diederich [37], where the lowest AIC value indicates the best model fit, we take the model for participants inside the Grand Mosque to be better than that for those in the plaza. It also has some larger β values. However, importantly, only the model for those on the plaza demonstrates the connection between shared social identity and giving social support. Consequently, only this model has an indirect effect from perceived support to giving social support.

(iii) Alternative models

To explore the order of the model variables, we also tested alternative models to explain giving social support. First, we tested a model from social identification with the crowd

Table 4. Linear model of predictors of reported giving social support. $R^2 = 0.09$ for step 1; $\Delta R^2 = 0.09$ for step 2; $\Delta R^2 = 0.17$ for step 3. s.e., standard error.

	step 1					step 2					step 3				
		ç					q					Q			
	q	B.	β	d	95% Cl for b	q	B B	β	þ	95% CI for b	q	B B	β	d	95% CI for b
constant	5.48	0.25		< 0.001	(4.99, 5.96)	5.46	0.25		< 0.001	(4.97, 5.95)	3.36	0.32		<0.001	(2.73, 4.00)
age group	0.07	0.03	60:0	0.004	(0.02, 0.13)	0.07	0.03	0.08	0.007	(0.02, 0.12)	0.05	0.03	0.06	0.053	(<-0.01, 0.10)
gender	-0.15	0.05	- 0.09	0.003	(-0.25, -0.05)	-0.14	0.05	-0.08	0.007	(-0.24, -0.04)	- 0.13	0.05	- 0.07	0.010	(-0.23, -0.03)
education	0.04	0.02	0.07	0.018	(0.01, 0.08)	0.05	0.02	0.08	0.015	(0.01, 0.08)	0.04	0.02	0.07	0.016	(0.01, 0.08)
language (French versus	— 0.58	0.12	— 0.20	< 0.001	(-0.81, -0.35)	-0.53	0.12	-0.18	< 0.001	(-0.77, -0.030)	-0.28	0.12	- 0.09	0.019	(-0.51, -0.05)
rest)															
Hajj service (non-Arab	0.01	0.12	< 0.01	0.954	(-0.22, 0.24)	0.02	0.12	0.01	0.863	(-0.21, 0.25)	- 0.04	0.11	- 0.01	0.731	(-0.26, 0.18)
African versus rest)															
performed Hajj before	-0.20	0.05	- 0.11	< 0.001	(-0.31, -0.10)	-0.20	0.05	-0.11	< 0.001	(-0.30, -0.09)	-0.16	0.05	- 0.09	0.002	(-0.26, -0.06)
acquiescence	0.13	0.04	0.09	0.001	(0.05, 0.20)	0.11	0.04	0.08	0.009	(0.03, 0.18)	0.09	0.04	0.06	0.027	(0.01, 0.16)
estimated density						0.01	0.02	0.01	0.685	(-0.02, 0.04)	0.01	0.01	0.03	0.327	(-0.01, 0.04)
(persons per metre ²)															
Mosque versus plaza						0.14	0.06	0.08	0.012	(0.03, 0.25)	0.13	0.05	0.08	0.011	(0.03, 0.24)
social identity with crowd											0.25	0.04	0.23	<0.001	(0.18, 0.32)
good Muslims											0.11	0.04	0.09	0.007	(0.03, 0.18)

to giving social support via perceived social support and the perception of others as good Muslims, again including the covariates of education, language, prior experience of the Hajj, and acquiescence (figures 7 and 8). The model fit for this version of the model for participants who responded inside the Grand Mosque was AIC = 18 250.279, RMSEA = 0.067, SRMR = 0.060, CFI = 0.913, $\chi^2_{99} = 285.992$, p < 0.001, and for participants in the plaza, $AIC = 32\,864.698$, RMSEA = 0.089, SRMR = 0.065, CFI = 0.850, $\chi^2_{99} = 681.643$, p < 0.001. Second, we tested the model with the order of the original mediator variables reversed, from perceived social support to giving social support via social identification with the crowd and the perception that others are good Muslims (figures 9 and 10). The model fit statistics for respondents inside the Grand Mosque were AIC = 32835.680, RMSEA = 0.086, SRMR = 0.056, CFI = 0.857 $\chi^2_{99} = 652.626$, p < 0.001, and in the plaza, AIC = 18 233.213, RMSEA = 0.064, SRMR = 0.048, CFI = 0.894, χ^2_{99} = 28.926, p < 0.001. Overall, the fit statistics for the alternative models, though better on some criteria, were comparable and not an improvement on the hypothesized model.

4. Discussion

According to both participants' perceptions and researchers' estimates, the Grand Mosque was the most crowded location at the Hajj. Neither location (Mosque versus plaza) nor crowd density predicted perceptions of social support (which were relatively high across the sample). Examining participants' reports of their own cooperative behaviour allowed us to look more closely at the possible psychological processes involved. Participants reported giving more social support in the plaza than in the Mosque. The shared social identity variables seeing others as good Muslims and identification with the crowd—were the strongest predictors of this self-reported cooperation. However, it is important to note that perceptions of cooperation by others were the same across locations, and the reports of giving help (and indeed the other measures) were all high both inside and outside the Mosque.

We found evidence for a process of cooperation involving shared social identity. In the first place, seeing others' supportive behaviour predicted perceiving others as good Muslins and identifying with the crowd. In the second place, identification with the crowd predicted giving social support—at least on the plaza. Moreover, on the plaza there was a significant indirect effect from seeing others' cooperative behaviour via shared social identity (identification with the crowd) and giving social support.

There is a substantial research literature on the spreading of cooperative (or 'generous') behaviour (e.g. [38,39]). The mechanism of 'spread' suggested by our analysis—shared social identity—is an alternative to those accounts that conceptualize it as form of 'contagion'. The 'contagion' concept implies that such behaviour spreads as a form of mimicry, or at least with little discrimination. By contrast the present account focuses on the way that others' (cooperative) behaviours tell us something about their category membership: whether they embody the values of a social category and indeed whether they are in our own group; if they are 'us', we feel more motivated to give them social support [29–31].

We suggested in the Introduction that experiences in the Mosque might be more varied than on the plaza: seeing the Ka'aba produces the most intense positive emotional experience, but there is also competition to get close, and some get inside only to find their view obscured. The present findings are consistent with the view that this 'mixed' experience is associated with less cooperative behaviour compared with being on the plaza; perhaps the more relaxed and 'homogeneous' experience of the plaza enables greater cooperation. This difference in behaviour and process between the two locations supports the overall thesis of this article that the psychological is in part a function of the spatial.

A limitation of the study is that we have no direct measures of competition or other mediating factors in the Mosque. We do know, from the analysis, that simple crowd density does not seem to differentiate behaviour in the Mosque versus the plaza. It may be possible to use the current dataset to explore further some of these questions, since it is now publicly available. However, we suggest that a different kind of study may be needed to examine the phenomenology of the Mosque experience to determine process in more detail. For example, rather than questioning pilgrims, research could take the form of an ethnography, in which the observing researcher acts as the research instrument.

Many of the questionnaire items were constructed for this survey (when no established scales were available), and for practical reasons some measures were brief. More importantly perhaps for our claims about process, this study was cross-sectional. Clearly, the correlational nature of the design means that, while there is evidence for the process of cooperation specified here, other configurations of the variables are possible. For example, we know from elsewhere that shared identity enhances expectations (and hence perceptions) that others will be supportive [6,7]; and we can infer that since giving social support is likely to encourage others to do the same, other starting points than perceived social support are possible. While the model tested here was a little better than the alternatives we looked at, other alternatives are possible. The present design decision was again due to practical constraints, for running a panel study (to allow cross-lagged analysis) presented insurmountable difficulties.

Finally, this analysis had a relatively narrow scope. There are other collective-behavioural features of the Hajj that are practically as well as theoretically important which we could have investigated. These include the preference of Shia Muslims to pray in the open at the Mosque, for example. A prediction of self-categorization theory would be that, by gathering together to pray in the open, the Shia identity might become more salient than the superordinate Muslim identity, due to both comparative and normative fit [23]. However, investigating this question must wait for a future study.

The relation between architecture and (collective) behaviour has long been noted, both generally [40] and in relation to Islamic design [41], with its characteristic feature of symmetry. Open spaces, for example, can facilitate interaction [42], and the design of the Grand Mosque and plaza offer examples where this is the case. There is also a clear association between certain architectural features and (disordered) behaviour in emergency evacuations [8]. Disasters at Hajj locations and other pilgrimages have been linked to collective behaviour [43], often with the implication that crowds at these holy sites lack the critical judgement necessary for coordinated conduct [7,13,43]. The present study suggests an alternative view of the relation between collective behaviour and disaster risk reduction in crowded locations, which side-steps attempts to define rationality (versus 'panic') in these contexts (cf. [8]), through the use of the concept of social identity. As well as explaining disasters, we need to explain the fact that most of the time the Hajj crowd is orderly. Shared social identity in a crowd is an established predictor of cooperative and coordinated behaviour and can therefore help explain that orderliness. Space and place (for example carrying out rituals in spiritually important buildings) can serve to enhance the salience of social identities [44]. These points are relevant to the planning for mass gatherings [34], to crowd safety management training [7], and in computer simulation in planning [45]. Most crowd plans and simulations assume simply that a crowd is a large number of people in the same place. The social identity concept suggests, and our findings evidence, that collective behaviour-behaving as a crowd, rather than simply as individuals in the same location-varies according to the context, and therefore that this should be a fundamental assumption of planning.

5. Conclusion

A questionnaire survey of 1194 pilgrims at the Hajj to Mecca found that pilgrims perceived the Grand Mosque as a very crowded ritual location. Pilgrims were more likely to report giving support to others in the Mosque itself than in the plaza outside; crowd density did not appear to be a factor in the explanation; shared social identity explained more of the variance than both location and density. There was also evidence of a process of cooperation: perceiving others give support predicted shared social identity which predicted giving help to others. This predictive pattern only occurred in the plaza, and suggests the role of place and space in modulating identity processes.

Ethics. The study protocol was approved by the Ethical Committee, Custodian of the Two Holy Mosques Institute of Hajj Research, Umm Al-Qura University, Mecca, KSA and by the University of Sussex, Brighton, UK in July 2012. All participants provided their written informed consent before participation.

Data accessibility. The original SPSS dataset is available on Figshare: https://figshare.com/articles/HAJ3317aORIGINALDATASET_sav/5406403.

Authors' contributions. H.A.: research design, data collection, analysis, writing, data curation. J.D.: supervision, research design, analysis, writing. A.T.: analysis, writing.

Competing interests. We declare we have no competing interests.

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Endnotes

¹The Islamic calendar is lunar, so the date of the Hajj changes year by year in the Gregorian calendar. ²The Hajj rituals last for 5 days, but pilgrims gather in a crowd at the

²The Hajj rituals last for 5 days, but pilgrims gather in a crowd at the Holy Mosque to take part in *tawaf* in the days beforehand and immediately afterwards.

³It makes intuitive sense to assume that people willing to participate in a survey may be more dispositionally cooperative than others. Given that response rates correlated with age, education and gender, we compared participants in each of these on giving social support to test for demographic evidence of such a bias. See the electronic supplementary material for details.

⁴We report results for this analysis carried out without the covariates in the electronic supplementary material.

⁵See the electronic supplementary material for additional analysis in which we test a version of the model without the variable 'others are good Muslims'.

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Can we identify general architectural principles that impact the collective behaviour of both human and animal systems?

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The search for general common principles that unify disciplines is a longstanding challenge for interdisciplinary research. Architecture has always been an interdisciplinary pursuit, combining engineering, art and culture. The rise of biomimetic architecture adds to the interdisciplinary span. We discuss the similarities and differences among human and animal societies in how architecture influences their collective behaviour. We argue that the emergence of a fully biomimetic architecture involves breaking down what we call 'pernicious dualities' that have permeated our discourse for decades, artificial divisions between species, between organism and environment, between genotype and phenotype, and in the case of architecture, the supposed duality between the built environment and its builders. We suggest that niche construction theory may serve as a starting point for unifying our thinking across disciplines, taxa and spatial scales.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

1. Introduction

When René Descartes formulated 'mind-body' dualism, his aim was to distinguish humanity from the animal world, and at the same time to salvage a place for God in a material world. For the Cartesian, the duality is between mind and body—between the transcendent mind and the clockwork machinery of living things. This distinction, and the form of logical argument upon which it was based, has been taken up enthusiastically by a large strain of modern biological thought, which has sought to impose a host of its own dualities, among them the duality between organism versus environment, between phenotype versus genotype, categorical species from categorical species [1]. This has left a history of the biological and social sciences that is strewn with paradoxes [2]. As we do with the Cartesian duality between mind and body, we might ask whether the dualities that permeate modern biological thought help or hinder our understanding. Arguably, modern biology has yet to grapple critically with this question, which has led modern biology into a philosophical crisis [3].

Duality is also rearing its head in the emerging trend of biomimetic architecture [4]. Like other forms of biomimicry, biomimetic architecture is motivated by a desire that human architecture should draw inspiration from the constructions of 'animal architects', such as the remarkable structures built by social insects [5,6]. The implication is that there is a fundamental duality between animal architects and the human variety. That we should draw inspiration from 'designs' in nature rests upon a Darwinian argument: that natural selection has shaped these

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2

structures to levels of optimality and economy that human architects would do well to emulate [7].

However laudable the inspiration, it is worth remembering that modern Darwinism is permeated with its own pernicious dualities: of genotype versus phenotype, of organism versus environment, to name two, which has left the landscape of modern Darwinism strewn with its own paradoxes [3]. These ramify into biomimetic architecture's own dualities: that human architecture is somehow radically distinct from other 'architectures' in nature, and that there is a fundamental distinction between the built environment and the agents that build it. Here, builders (agents) construct an environment in which the builders live. The built environment becomes thereby a 'machine for living', an object external to its inhabitants, that works to enable the inhabitants to live comfortably. The building does so by controlling flows of matter and energy between the environment and inhabitants so that the inhabitants' physiological needs can be met: suitable flows of heat, fresh air, moisture and information. As a Cartesian might argue that the body is a machine that houses a separate and transcendant soul, so the biomimetic architect casts the building as a machine that houses a separate and living being.

Add to this the materialistic logic that pervades modern Darwinism, and the perniciousness only deepens: a machine (a building) is designed to mimic another machine (an inhabitant). This is the sterile logic of Le Corbusier and the Bauhaus: machines to house interchangeable machines [8]. Which brings us directly to the question: what is biomimetic architecture intended to mimic? Is it living 'machines', or is it the unique phenomenon of life itself? This, in turn, prompts another question: if there *is* something distinctive about living nature that transcends the machine metaphor of life, what precisely would that be? And what are the prospects for incorporating it into architectural practice? Is there something beyond the building-as-machine metaphor?

2. Cognition, the extended mind and the extended organism

Arguably, what makes living systems unique is that they are *cognitive* systems [3,9,10]. Machines, in contrast, cannot be cognitive systems. While machines can imitate some aspects of cognitive agency (the *raison d'être* of artificial intelligence), they cannot be cognitive systems in the same way living systems are. For example, some aspects of cognition, such as constructing sensory representations, processing the information in those representations and acting upon them, are certainly amenable to automation. Yet cognition also includes phenomena such as intentionality and creativity [11], which seem less amenable to reduction to computation. Living cognition in full seems tied inextricably to the uniquely living phenomenon of mind. In short, living cognitive systems are a kind of embodied mind.

In the cognitive sciences, embodied cognition was introduced as a theoretical complement to traditional dualist interpretations of mind and body [12]. Broadly stated, the theory holds that cognition is shaped by an organism's body in such a way that sensory and perceptual systems, as well as the motor systems, determine how concepts and categories are formed and influence reasoning and problem-solving (e.g. [13–16]). Closely related to this is the notion of extended mind and situated cognition. These address how organisms manipulate the environment in service of cognition to offload and scaffold cognitive processes [14,15,17–19]. Stated most broadly then, embodied cognition and extended mind are important theoretical contributions to our understanding of how brain, body and environment interact, in that they explain how sensorimotor capabilities, embedded in some natural context, determine thought and action. For a review of developments across this line of theorizing, the reader is referred to Newen *et al.* [20] and their compendium of papers on embodied, embedded, enactive and extended cognition.

These notions of 'embodiment' and the 'extended mind' now form the dominant paradigm in cognitive science. The same logic can be extended to swarms of autonomous agents, so-called swarm cognition, which forms the basis of many theories of emergent systems, such as organisms and organism-like systems (for example, social insect colonies) or ecosystems [21-23]. In contrast to most evolutionary thought, which draws a sharp distinction between organism and environment, theories of embodied mind treat organism and environment as interactive and inseparable. Not only do organisms work and evolve to fit into an environment (adaptation), organisms actively modify the environment to suit themselves: adapting the environment to the organism. This dissolves one of biomimetic architecture's pernicious dualities: environment and organism are inseparable, two aspects of a single phenomenon: adaptation.

Turner has argued that adaptive systems are necessarily cognitive systems [3,11]. An adaptive system must *know* the state of the relationship between organism and environment, and *know* what work must be done to bring both into coherency. This is goal-directed intentional behaviour (the literal meaning of the term 'adaptation': toward aptitude), and it undermines biomimicry's self-imposed duality between human architecture and 'natural' (i.e. non-human) architecture. If adaptation is the driver of evolution, the tip of the evolutionary spear, so to speak, then there is no distinction to be drawn between human builders and animal builders. The constructions of both are reflections of a universal cognition that distinguishes all life.

For Turner, this goal-directedness is embodied in a radical interpretation of Claude Bernard's concept of homeostasis [23]. What follows logically from this is Turner's notion of the extended organism, which abolishes the duality between organism and environment: the environment is as 'alive' as the organism inhabiting it [1]. This opens up a new metaphor for the notion of biomimetic architecture [24]. Now, rather than speaking of the building-as-machine, we may speak of the building-as-organism, a vital extension of the organism's own physiology. Now, the built environment and organism are partners in a physiological conspiracy (they literally 'breathe together'), both dynamically adaptable and evershifting, all serving the same fundamental aim of homeostasis [25]. The physiological conspiracy drives the adapted form forward in time, its persistence serving as a kind of evolutionary fitness.

Humans, along with social insects (bees, ants, some wasps and termites) provide some of the most dramatic examples of this physiological conspiracy, and it has obvious relevance for biomimetic architecture: what if our constructions mimicked the dynamic interaction of organism, environment and built environment that occurs routinely in nature? In this paper, we investigate the parallels that can be drawn between social insects and humans in their adaptation of the environment through building, and the way that in turn these artificial environments support the social interactions of their communities or colonies. We ask whether there is an underlying theoretical framework through which the building behaviour of these different phyla and their social-functional interactions can be unified.

We develop our discussion in three stages. First, we look at the logical restrictions on what it is possible to construct. Next, we look at the effect of different sensory and bodily competencies on shaping organisms' interactions between each other and their environment. We consider what this might imply for differing cognitive models of their environment-the 'umwelt'-of different species, and the different possible social structures that might be perpetuated thereby, through the constraints imposed by configuring the environment and its interaction with individual and group behaviours. Finally, we discuss the role of the built environment in the reproduction and evolution of social forms across phyla. This last, we propose, may help account for human social and cultural evolution proceeding at a rate far faster than genetic evolution, while also accounting for social forms outlasting, on occasion, the lifespan of the individuals from which they are composed.

3. The logic of the constructible

The act of construction can be thought of as inherently simple while, at the same time, giving rise to the largest and most complex of human artefacts. Piling stones upon one another, for example, is a primitive repetitive building technique. Out of this repetition can emerge buildings of exquisite design, as in the mortarless walls of the Great Zimbabwe [26]. By what logic can the repetitive act of piling stones upon one another connect to the sublime structures of the Great Zimbabwe? We argue that it is impossible to do without an appreciation of the cultural and cognitive agency of its builders [27,28].

Are humans unique in their ability to create a Great Zimbabwe out of the repetitive process of piling stones upon one another? Arguably, no. In the world of social insects, for example, constructed nests can also be extremely large and spatially complex in their construction, rivalling human constructions in complexity and beauty. Social insect nests, too, may be constructed by the repetition of many relatively simple repeated actions. Individual insects may pick up grains of sand, transport them somewhere, and lay them down again, either glued in place with a kind of mortar, or simply laid down with a dollop of saliva. We ask: how does this simple and repetitive act produce the sublime architecture of the leaf-cutter ant nest [29,30]? As with the Great Zimbabwe, there seems to be an inseparable cognitive and cultural dimension to the construction of the social insect nest, even as the context is radically different.

What logical inference should be drawn from this? For example, should we highlight the dissimilarities of context—form and function—and conclude that humans and leaf-cutter ants are radically different forms of architect? Or should we highlight the similarities—the similar processes of construction—and conclude that leaf-cutter ants and humans are the same kinds of architect? In short, what is the logic of the constructible environment? We explore this question through three examples: Guy Theraulaz's agentbased model, exemplified by the constructed nests of the termites *Apicotermes*; Scott Turner's notion of the extended organism and swarm cognition, developed in a different termite species, *Macrotermes*; and Bill Hillier's conception of beady-ring settlements in the South of France.

4. Agent-based model

Lijie Guo, Guy Theraulaz and colleagues describe a simulation of termite nest building, focusing on the remarkable nest of the termite genus *Apicotermes*. The *Apicotermes* nest is made up of a spiralling series of galleries cut through by ramp-type structures and columns. Guo, Theraulaz and colleagues show that the nest's characteristic helicoidal and linear ramps can result from a particular suite of cellular building processes [31].

Their simulation entailed termites whose building behaviour consists of moving earth from the floor to the ceiling of the galleries. They show that changing the parameters for a model for nest construction by *Lasius niger* ants [32] can create the characteristic helicoidal structure of the *Apicotermes* nest. The constructing agents, the individual termites, are therefore agents whose behaviour is governed by simple rules of interaction, with other agents programmed with the same rules, and with the built environment they create (figure 1).

The *Apicotermes* nest is a marvellous example of how multitudinous agents driven by simple behavioural rules of repetitive aggregation can produce objects of great beauty and complexity. Yet is it appropriate even to speak in such terms? Is there an aesthetic of nest construction that governs the behaviour of the *Apicotermes* swarm? In the Darwinian metaphor for biomimetic architecture, the answer to this question must be 'no': it is functional effectiveness—adaptation of some form—that is the driver. *Apicotermes* nests therefore exist in their present form because nest form has been refined by generations of natural selection from ancestral species with more primitive nests [33,34]. The evolutionary trajectory toward the *Apicotermes* nest's present sublime form has been driven by incremental accrual of fitness advantage.

It has proven difficult to identify what these advantages might have been, however. Schmidt attributed the form to superior ventilation and protection from predators [33,34], with superior nest ventilation being the favoured explanation [35]. There is little evidence to support that claim, however. Theraulaz and colleagues have modelled the emergence of the *Apicotermes* nest using principles of self-organization and self-assembly [36,37]. He attributes the emergence of complex nests to the greater complexity of information exchange and versatility of behaviour that accrues to increases in the colony population [38,39]. In this sense, it is versatility *per se* that has been the fitness advantage.

We might reconstruct Theraulaz's 'logic of the constructible' in this way. Construction is explained by rules of interaction of building agents, with both other building agents and the structures that they build. Increased complexity arises from the nonlinear dynamics of the interaction between agents and the environment they build [40–42]. There remains at the heart of this logic another pernicious duality: function is divorced from structure. The aesthetic of the *Apicotermes* nest is an accidental outcome of these evolving rules of interaction, producing structures that garner selective advantage through some unidentified adaptation.



Figure 1. The construction of the helicoidal ramp structure of the *Apicotermes* nest. (*a*) (top) Ramps (visualized by red dots) and (bottom) a helix. (*b*) Simulation of the nest construction dynamics (figures 2 and 5 from Guo *et al.* [31]). Reprinted with permission from Guo *et al.* [31] (Copyright © 2016 IEEE). (Online version in colour.)

5. The extended organism and the aesthetic of niche construction

A different approach is Turner's extended-organism idea [1,43], which came out of his work on the mounds built by the fungus-cultivating termites of the Macrotermitinae, specifically the mound-building termites of the genus Macrotermes. Turner builds on Odling-Smee, Laland and Feldman's notion of niche construction. Where a conventional interpretation of Darwinian evolution holds that organisms evolve to fit their environmental context, niche construction theory [44] recognizes that as often as not organisms actively adapt their immediate environment to suit their own needs. The extended-organism idea is the physiological dimension of Dawkins' notion of the extended phenotype [45]. This idea treats the mound as essentially a superorganismal organ of physiology, as much alive as the termites that build it. This incorporates a directed dynamism to the mound structure, with a much more fluid interaction with the environment than strictly agent-based models, like those of Theraulaz and Bonabeau, allow [38]. So, for example, Turner and colleagues have identified several drivers of mound building and disassembly [46], which relegates the concept of stigmergy (in Grassé's original sense of the term: 1959 [36]), centrally important to the self-organization concept, to a limited context of mound repair. Such variation can be modelled using agent-based algorithms, as Jost et al. [47] have done for the influence of air currents on architecture of ant nests. In the extended-organism metaphor, however, variation of mound

architecture arises from a rich interplay of building behaviour and the cognitive environment enclosed by the built structure. The difference is, in part, philosophical: cognition embodies a kind of striving that agent-based models do not consider [11].

So, for example, two species, *Macrotermes michaelseni* and *Macrotermes natalensis*, each build distinctive mounds: *M. michaelseni* builds conical mounds topped by a tall spire while *M. natalensis* build conical mounds without the spire. These differences in mound architecture can be attributed to differences in swarm cognition: *M. michaelseni* construction is influenced more strongly by water transport and regulation of nest moisture, while *M. natalensis* construction is influenced more strongly by stigmergy and mound repair (figure 2).

So far, this conception is fully consistent with the agentbased model of nest construction (e.g. [47]). However, the cognitive dimension of the extended-organism idea embodies an aesthetic of construction. The source of the aesthetic dimension is homeostasis, the signature idea of the nineteenth century contemporary of Darwin, Claude Bernard. Bernard was a physiologist, not an evolutionist, architect or student of social insects. Yet Bernard's conception of homeostasis colours our interpretation of all these fields.

Bernard regarded homeostasis as life's fundamental property, that which distinguishes life from non-life (the 1927 reprint of Bernard's 1865 *An Introduction to the Study of Experimental Medicine* [48]). This is an essentially vitalist idea that is quite at odds with our modern conception of homeostasis. Our modern tendency is to reduce homeostasis to cybernetics, to elucidate the mechanisms that produce regulation



Figure 2. Characteristic mound architecture of two common *Macrotermes* species (a) *M. michaelseni* and (b) *M. natalensis* (Photo credit J. S. Turner). (Online version in colour.)



Figure 3. The cognitive world of the *Macrotermes* extended organism. Termites form a cognitive representation, at both individual and swarm level of a 'desirable' environment of steady environmental conditions. These conditions are the result of a constructed environment based upon the engineered porous interface of the mound surface, which acts to filter energy in turbulent external winds.

of a specific property of the body, say, temperature. Bernard's own conception of homeostasis turns the cybernetic idea on its head: whereas the cybernetic conception regards homeostasis as the outcome of mechanism, Bernard regarded mechanism as being the outcome of homeostasis.

Among other things, Bernard's conception of homeostasis broadens the scope of the phenomenon of cognition to include the ability to shape environments according to some mental representation. This is where the distinction from automatabased models emerges. While swarms of automata can shape environments, they cannot properly be said to *want* to shape environments in a particular way: they are machines acting out an algorithm. In living cognitive systems, while mental representations of the environment often reflect the environment, they need not do so, and when they do not, cognition comes to embody intentionality and creativity, both a kind of wanting [49]. Homeostasis, in the Bernardian sense, opens the door to novelty and appeal: an aesthetic, in short (figure 3).

In *Macrotermes*, this essentially aesthetic tendency is revealed in the phenomenon of mound repair. An environment that 'appeals' to termites includes still air, and steady concentrations of oxygen, carbon dioxide and water vapour (humidity). An 'unappealing' environment is marked by unpredictable and rapid changes in the environment: slight gusts, fluctuations of oxygen and carbon dioxide concentrations, or humidity. These disturbances usually come about in the aftermath of damage to the structured boundary of the mound, which is porous and modulates the effects of the windy and turbulent external environment. The response of termite swarms to any disparity



Figure 4. Mound-environment homeostasis as resolution of cognitive disparities. A breach in the mound disrupts the internal environment of the mound, which leads to a cognitive disparity at both individual and swarm levels. This initiates a programme of mound repair, which ultimately resolves the cognitive disparity.

in appeal is to mobilize a colony-wide project to reshape the environment to restore the colony environment to an appealing state. This includes ongoing colony-level decision-making, which can persist over several months, even years, far beyond the lifespan of any individual worker termite [46] (figure 4).

In this instance, the duality between organism and environment dissolves. The termites, nest and mound constitute a physiological conspiracy to co-opt and tame environments to the colony's aesthetic demands.

One can object to the notion of termites, or any agent-based self-organized system, being motivated by aesthetics. Occam's razor, for example, would seem to favour the simpler explanation of rules of interaction between essentially robotic agents and their environments (in the sense of Jost *et al.* [47]), without introducing complications such as aesthetics. It is a valid point of difference, and a frankly philosophical one, delineated by the question: can one explain the behaviour of any living system without accounting for life's fundamental attributes of cognition, homeostasis and striving [2,3]? It is worth noting that Occam's razor is not simply an appeal to favour

the simplest possible hypothesis: it is an admonition to not generate complex hypotheses *without necessity* [50]. We argue that cognition, and all that is implied by that, is just such a necessity. Without accounting for that, there can be no unifying principles that explain the built environments of organisms ranging from insects to humans.

7. Beady-ring settlements

Bill Hillier and colleagues' approach to human settlements was different [51]. They aimed to develop an account of the vast array of human settlement forms found in the archaeological and anthropological record. They developed an ideographic language in which elementary generators such as a carrier space, the relation of containment and a boundary, are brought together in a logical syntax. They show how this language can be used to express, in a greatly simplified way, the main spatial features of a wide range of different built forms. This is the 'syntax' of space syntax. At its simplest level, they show how a process of rule that restricted random



Figure 5. Beady-ring settlements (photo credit Bill Hillier), Map of Les Yves 1961 (figure 9 from Hillier & Hanson [51], p59). Reprinted with permission from Hillier & Hanson [51] (Copyright © 1989 Cambridge University Press). (Online version in colour.)

aggregation of buildings generates the spatial characteristics of a class of what they called 'beady-ring' settlements [51].

The beady-ring settlements Hillier describes occur in the Vaucluse region of Southern France, and are small hamlets characterized by an aggregation of houses usually forming a ring of circulation around a central clump of buildings, with several routes out to the surrounding countryside. The ring of circulation is composed of wider and narrower spaces—the 'beads' on the ring—and has the property that all locations are directly overseen by entrances to the houses (figure 5).

Hillier & Hanson [51] describe a rule restricted random process, involving aggregation of open space-built form dyads, that gives rise to these features. Starting with an open spacebuilding pair, linked by the building entrance, additional dyads are aggregated by linking open space to open space (rather than building to building) (figure 6). While this generative rule gives rise to 'phenotypic' differences, that is differences between individual settlements, the 'genotypic' properties remain, such as a continuous ring of open space, fatter and thinner pieces of open space and the continuous relationship to building entrances. However, above a certain scale these settlements cease to be lifelike. In larger settlements in the region, we notice greater regularity with streets extending linearly and a deformed grid appearing.

Longer statements in Hillier and Hanson's recursive language give rise to more ordered spatial systems including central 'squares', and axially extended streets and grids. The notions of linear extension and of convexity of space are shown to emerge from rule restricted random processes (figure 7).

These properties of linear extension and convexity carry direct social consequences. Since we are interested in what can be constructed that potentially has a systematic effect on social outcomes, we can restrict our consideration to some specific aspects of what it is possible to build. For example, we might consider that everything that one can do to configure space becomes meaningful in terms of some specific mode of perception. Thus, for the modality of human vision the constraint imposed by construction of a wall is to obstruct long distance lines of sight and movement. The way that walls are configured-that is constructed with relation to each other-affects the inter-visibility of points in space. For example, if walls are constructed to create an enclosure, the effect is to define two regions in the floor plane: those inside the enclosure and those outside. Points inside the enclosure have the significant property that if point A can see B and B can see C, then A and C can also see each other. The same does not hold for any three points in the exterior region. Here it will always be possible for A', B' and C' to be located so that the walls of the enclosure hide one or another pair of points from each other. Within a sufficiently small distance of the enclosure it is possible that none of the three points can see each other. For the modality of hearing however the effect is different. Sound can travel around corners and so, in principle, it is possible for A', B'



Figure 6. Four stages of a computer generated of a beady-ring architecture (figure 11 from Hillier & Hanson [51], p60). Reprinted with permission from Hillier & Hanson [51].

and C' although not inter-visible, to be within earshot (figure 8).

The effects described above result from the relationships between stationary individuals (A, B and C), and their individual relations to the boundary of the environment.

There is a second kind of effect that applies when we consider mobile individuals, and how their patterns of movement bring them together, or keep them apart, in space. Consider, for example, the effect of changing the aggregation rule for the beady-ring settlement from 'open-space links to openspace' to 'building links to building'. The result is a settlement characterized by tree-like spaces and cul-de-sacs. Here the configuration of the environment determines the network properties of the space, and this imposes strong constraints on patterns of movement. These in turn affect how individuals are brought into proximity as they move through the environment. For example, if the network is 'tree-like' there will be just one route between any origin O and destination D, however if the network is 'ringy', then there may be numerous different routes between O and D (figure 9).

These properties have direct effects on the probability that any two individuals will be co-present in space. They also have a direct effect on which spaces are more likely to carry movement and which will host higher numbers of co-present individuals. In this way, the spatial configuration of the environment would be expected to exert a probabilistic effect on co-presence and awareness, and, all other things being equal, to constrain and give a pattern to the probability of social interaction.

8. Perception and the umwelt of species

We have now come to the largest pernicious duality: are humans distinctive from the rest of living nature? This prompts the question: if so, how? The answers to these questions colour our perception of architecture, human and otherwise, and how they relate to one another. These perceptions, in turn, cast the whole premise of biomimetic architecture into a new and critical light.

The basic premise of biomimetic architecture is that humans have strayed from the basic principle that shapes the rest of living nature, namely evolution through Darwinian natural selection. This has honed living nature to a high degree of efficient use of energy and materials: 'billions of years of research and development', as the literature of the Biomimicry Institute vividly puts it. This prompts the question: are human constructions so radically different in form and process that mimicking the rest of living nature should even be a consideration? Or is there some fundamental unity in both human and natural built environments?

The three examples we have outlined-swarms of artificial agents, cognitive swarms of termite builders and generations of beady-ring settlements-offer different perspectives to these questions. Networks of artificial agents, for example, evince emergent properties that are the result of rules of association: algorithms. Inputs to these algorithms of construction are information from the environment, which include both built structure and other agents. Outputs are emergent phenomena of architecture and self-organization. This perspective is closely in line with biomimicry's conception of nature as selectively-honed perfection. Agentbased models consist of machines that behave according to particular suites of input/output relations. In any particular environment, these rules either work well or they do not. To the extent that there is genetic variation in these rules, natural selection will enhance the persistence of some of these variants and diminish the persistence of others. Endless repetition of this process produces the 'billions of years of research and development'. There is no place



Fig. 23 Elementary formulae and recursions.

List of elementary formulae

 $Z_{1}:y$ $Z_{2}:X$ $Z_{3}:(Xy)$ $Z_{4}:(X \circ X)$ $Z_{5}:(X X \circ y)$ $Z_{6}:(X \circ XX)$ $Z_{7}:(XX \circ XX \circ y)$ $Z_{8}:(X \circ X \circ XX)$





Figure 8. Interactions of individuals are constrained by the morphology of walls in their environment. (Online version in colour.)

in this scheme, however, for the agents except as vehicles for implementing algorithms: the agents do not 'know' whether they are constructing an apt environment, because they incapable of 'knowledge'. They are mere machines.

In contrast, both termite swarms and beady-ring settlements evince a fundamental element of cognition, self-



Figure 9. Movements of individuals in a ringy and tree-like settlement. (Online version in colour.)

awareness and intentionality that is lacking from automaton agent-based models. Swarms of termite builders, for example, draw the built environment into a kind of physiological conspiracy. The mound is an extension of the termite swarm superorganism, managing flows of matter and energy between swarm and environment in the same way that, say, the intestinal epithelium does. Termites not only sense the environment and communicate and influence one another's behaviours

through their own sensory and cognitive systems, they construct a mound that modulates and encodes information as would, say, sensory structures in the termites themselves. The mound is an expression of cognition as much as the human eye is an expression of the visual cognitive system. Beady-ring settlements, for their part, develop according to the inhabitants' cognitive perceptions of the built environment, which are shaped to expand perception of the environment, including lines-of-sight and acoustic channels, determined in part by visual fields in which linear extension and forward motion come together. Linear street systems and corridors are the spatial counterpart of this set of perceptual competences.

It follows that the construction of the built environment will reflect mostly the perceptual capabilities of the agents, rather than the perpetual fine tuning of the endless beta versions of the algorithms that shape the behaviours of agent swarms. The built environment thus combines Uexküll's umwelt and innenwelt [52]. Termite swarms, for example, inhabit a much different perceptual world than humans. They have an entirely different suite of sensory capabilities-no vision, a rich chemical language, acute vibration perception, hyper-sensitivity to temporal perturbation in the environment-and this results in a very different built environment from those constructed by humans. For their part, humans have well-developed senses of binocular vision and binaural hearing that serves a sophisticated spatial perception. What is striking is not so much the differences in architecture-stark as they are-but their similarity: both are cognitive expressions of an extended organism. Termites and their constructed environments on the one hand, communities and their constructed environments on the other.

To a first order of approximation, the behaviour of a mobile individual subject with different perceptual competences will be constrained by the morphology of their environment as a function of their location, orientation, trajectory and speed of movement, their modes of perception (sight, hearing, touch, smell etc.), and the way these are integrated, the perceptual affordances of their anatomy (for example the acuity of vision, or angle of their visual field and mobility of their head), and the configuration and properties of the environment's boundaries [53].

In a social context, where numerous individuals inhabit the same environment at the same time, the location, behaviour and relationships to and between other individuals within the subject's field of awareness (each of whose behaviour is also a product of these constraints) must be added.

Finally, the individual's interaction with their environment, including that afforded by other individuals and groups, for higher animal species, must be thought of as passing through (at least) cognitive, affective and conative 'filters'. Thus, an individual's 'beliefs' about the world they perceive, their 'desires' and emotional state, and their immediate and longer-term 'intentions', will all affect how they interpret and respond to their perceived environment. At a social level, the functional programme or regime of a community or organization, and community culture and power relations can be thought of as contributing to this as well.

As a first-order approximation, this is of course a reductive model. The reality will be much more complex due to the feedback loops involved, the fact that individuals have memory and learn, and that, for humans at least, organizations and communities also develop social practices over time. The effect of cognitive, affective and conative filters must also be highly dependent upon previous experience and learning, something that would be expected to vary from subject to subject according to the social and cultural context of that individual's life experience.

In humans, as technologies have been invented, these have led to an elaboration of the human umwelt. Fundamental to this have been symbol systems and their manipulation. Written language and currency have led to socially stored memory and the creation of law and economic life, along with the apparatus of politics and the state. Written history and mythology have enabled both the great religions of the world and conceptions of nationhood, and so have also been instrumental in the development of the modern state. Mathematical notation has allowed the exploration of logical inference and of abstract or hypothetical worlds, and so the development of science. Science in turn has enabled new technologies with these making possible new forms of social structure. All of these have had direct impacts on behaviour; however, behaviour in turn produces social structure. It seems to be this series of feedback loops between different strata of the social that creates the human umwelt.

The specific contribution of this paper, in questioning the 'organism-environment' dualism, is to consider the built environment as an active element of this model, rather than a passive background to social action, or a merely cultural artefact whose social relevance is as a carrier of meaning. Unlike technologies that act purely as symbol systems and serve primarily to communicate meaning, the built environment also acts directly upon social relations. It should be noted that humans attribute symbolic meaning to almost everything they encounter, animate, inanimate, natural or artificial. In this the built environment is no different, and so also plays an important role in the communication of meaning, both intentionally on the part of its authors and as interpreted by its users. Our point here is that the built environment is more than this in that it also acts to make possible, or to inhibit, social relations themselves.

In drawing on Turner's notion of the termite nest forming part of the physiology of the 'super organism', we would draw by analogy here to human society. It would seem that the built environment, rather than affecting the physiology of a human superorganism, may affect its capacity in terms of distributed cognition. It is clear that the buildings and settlements we construct are the product of a set of social processes; that they are constructed by individuals and groups all subject to the perceptions and interactions described above; and, therefore, that they record in their configuration aspects of the social forms that generated them. It is also clear that through the mechanisms of awareness afforded by intervisibility and co-presence resulting from effects of configuration on movement routes, the built environment also holds the potential to generate and constrain social interactions and connections. In other words, it can act to reproduce a social form, or alternatively to generate new social forms.

It has not escaped our notice that this mechanism may help account for how it is that human social, cultural and technological evolution accelerated so rapidly after the first dense built settlements started to be constructed in the 10th millennium BC in the Eastern Mediterranean.

Data accessibility. This article has no additional data. Competing interests. We declare we have no competing interests.

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