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Review

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Author for correspondence:
Yara Khaluf
e-mail: yara.khaluf@ugent.be

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Scale invariance in natural and artificial collective systems: a review

Yara Khaluf[1], Eliseo Ferrante[2], Pieter Simoens[1] and Cristián Huepe[3,4]

[1]Ghent University—imec, IDLab-INTEC, Technologiepark 15, 9052 Gent, Belgium
[2]KU Leuven, Laboratory of Socioecology and Social Evolution, Naamsestraat 59, 3000 Leuven, Belgium
[3]CHuepe Labs, 814 W 19th Street 1F, Chicago, IL 60608, USA
[4]Northwestern Institute on Complex Systems & ESAM, Northwestern University, Evanston, IL 60208, USA

YK, 0000-0002-5590-9321; EF, 0000-0002-2213-8356; PS, 0000-0002-9569-9373

Self-organized collective coordinated behaviour is an impressive phenomenon, observed in a variety of natural and artificial systems, in which coherent global structures or dynamics emerge from local interactions between individual parts. If the degree of collective integration of a system does not depend on size, its level of robustness and adaptivity is typically increased and we refer to it as scale-invariant. In this review, we first identify three main types of self-organized scale-invariant systems: scale-invariant spatial structures, scale-invariant topologies and scale-invariant dynamics. We then provide examples of scale invariance from different domains in science, describe their origins and main features and discuss potential challenges and approaches for designing and engineering artificial systems with scale-invariant properties.

1. Introduction

The shift from centralized control to distributed and self-organized control in artificial systems has been one of the most significant trends in recent decades. This transition can be seen in a broad spectrum of artificial systems made of physical or virtual components. To fulfil their purpose, these systems must exhibit *collective behaviour* that results from a combination of multiple individual actions and interactions. For instance, a robot swarm can perform aggregation, collective motion or resource gathering as a result of multiple individuals autonomously taking decisions that are based on their local conditions—i.e. their direct neighbourhood and environment.

In nature, we find a large set of complex systems in which collective behaviour is observed. Such behaviour arises when parts of an organism coordinate to achieve a given function (e.g. cells self-organizing within a multicellular organism) or when organisms coordinate within a group (e.g. birds self-organizing in a flock or fish in a school). According to Brambilla *et al.* [1], these systems are characterized by three properties that engineers would benefit from replicating in decentralized designs: scalability, robustness and adaptivity. Robustness and scalability result directly from having redundant large-scale systems that achieve collective objectives without relying on global information. By contrast, achieving flexibility in artificial self-organizing systems is still a challenge.

To confront the design challenges of robustness and adaptivity, much can be learned from nature, since natural systems must be capable of achieving effective collective responses to a variety of external conditions and environmental changes in order to survive. Regardless of the specific mechanisms responsible for self-organization, a necessary condition for achieving such a collective response is having strong integration in the behaviour of the components of the self-organized system. In many cases, this integration must not depend on the spatio-temporal scale of the system, so that it can exhibit a collective integrated response to stimuli independently of the size of the system or of a given stimulus. We refer to such emerging collective dynamics as *scale-invariant*.
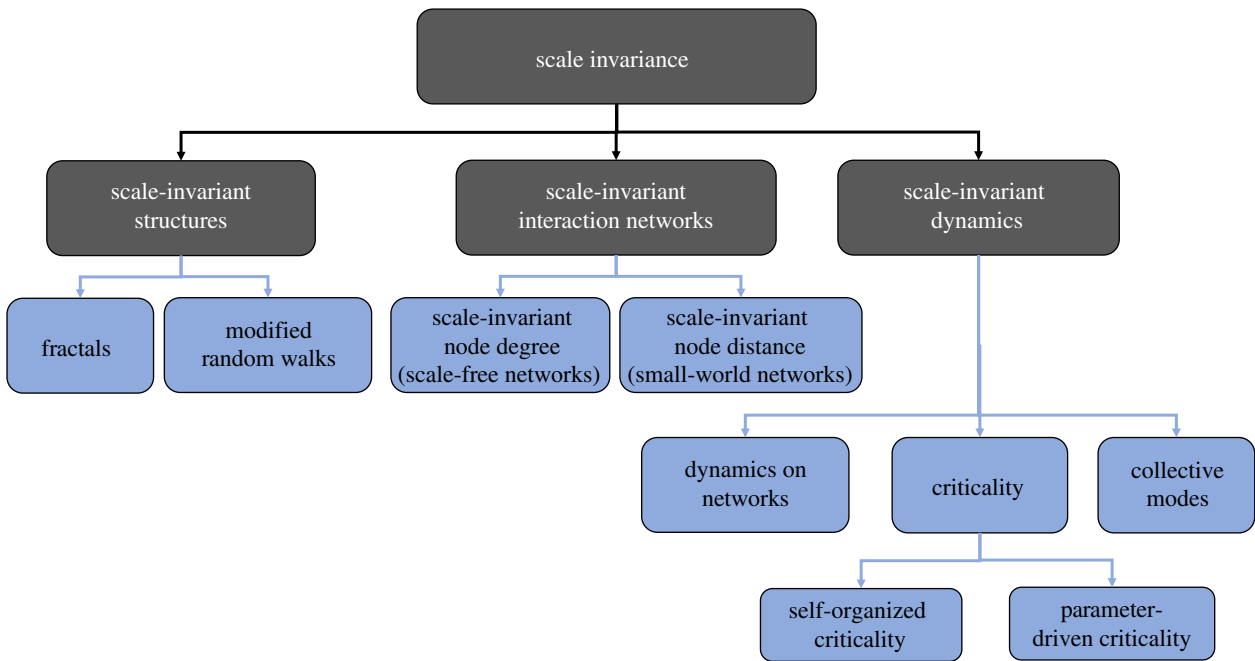
Figure 1. In this review paper, we identify three main types of scale invariance: (i) structures, (ii) topologies and (iii) dynamics, covered in §§3, 4 and 5 respectively. Fractals and modified random walks are examples of spatial and temporal structure that are scale-invariant. Scale-invariant topologies can be scale-invariant either in their node degree (scale-free networks) or in their intra-node distance (small-world networks). Scale-invariant dynamics can be induced either by the underlying scale-invariant topology, or by a mechanism called criticality (which can be either self-organized or induced by tuning an external parameter), or via collective modes. (Online version in colour.)

In this paper, we will review the scale-invariant properties exhibited by various systems in different branches of science and their underlying mechanisms, focusing on their potential application for the engineering design of flexible decentralized systems that respond coherently, as a single unit, to environmental challenges at all scales. We will start by, providing in §2, a mathematical framework and background materials on scale invariance. In §§3–5, we will describe different types of scale invariance found in nature, classifying them by their corresponding emergent scale-invariant features and by the underlying mechanisms responsible for them (figure 1). Section 3, will focus on scale-invariant spatial distributions, §4 on scale-invariant interaction networks and §5 on scale-invariant dynamics. For each type, we will present various examples found in the literature, stemming from diverse scientific fields, including physics, biology and social sciences. In §6, we will discuss potential applications of these examples from nature for engineering future artificial decentralized scale-invariant systems that are scalable, robust and flexible. Finally, §7 is our conclusion.

2. Background

The property of scale invariance describes situations where the essential structural and/or dynamical properties remain unchanged (i.e. *invariant*) when considering the system at different scales. In general mathematical terms, if we use $f(x)$ to describe the structure or dynamics of any system as a function of the (spatial or temporal) variable x, a scale-invariant system $f(x)$ must satisfy the condition

$$f(\lambda x) = C(\lambda) f(x). \tag{2.1}$$

Hence, if we consider a scale that differs from the original one by a factor λ, replacing $f(x)$ for $f(\lambda x)$, the property

described by f remains essentially unchanged; it is only multiplied by a scaling factor $C(\lambda)$ that does not depend on x. Although, in principle, $C(\lambda)$ can be any function, in practice, it is a power law for all the natural systems reviewed in this paper. We distinguish here two types of scale invariance, a *continuous scale invariance* in which λ can take any value and a *discrete scale invariance* in which it takes only discrete values, noting that the latter case may be in dissonance with some definitions found in the literature. In this paper, we thus define as scale-invariant any property that satisfies, for continuous or discrete values of λ and for a given $\Delta \in \mathbb{R}$, the power-law expression

$$f(\lambda x) = \lambda^{\Delta} f(x). \tag{2.2}$$

The continuous case is equivalent to stating that f is a homogeneous function. An example is any power law, since $f(x) = cx^p$ always satisfies equation (2.2) for $\Delta = p$. The discrete case corresponds to fractal-like, self-similar systems. We note, in addition, that some apparently discrete scale-invariant systems can actually correspond to specific statistical samplings of a continuous scale-invariant probability distribution. Therefore, if a discrete realization of a scale-invariant system is observed, it does not necessarily imply that equation (2.2) is satisfied only for a discrete λ, but could instead mean that $f(x)$ is a probability distribution and that we are observing a discrete statistical sampling of its values.

Scale-invariant systems typically have no characteristic scale, since any specific scale that defines them would have to appear in the function $f(x)$, making the transformation in equation (2.2) impossible. Such scale-invariant systems are thus often referred to as being *scale-free* (SF). From a system design perspective, this means that the property $f(x)$ holds regardless of the spatial or temporal scale. This also explains why power laws commonly appear when describing scale-invariant systems. Indeed, the

argument in most other functions (such as exponential or trigonometric functions) must have dimensionless units, and this can be achieved only by dividing x by another dimensional variable that defines a characteristic scale. Finally, we note that in real-world scale-invariant systems, this invariance can never cover *all* scales—there will always be physical cut-offs at very large and very small scales—but must still be valid over a broad range of scales.

All systems we review in this paper exhibit the above property of scale invariance. An important distinction that must be made is whether these systems are the result of biological evolution and adaptation or not. If this is the case, we can argue that these systems are 'guaranteed' to be optimally responsive to the environmental conditions, and therefore robust and adaptive. If instead such systems are not under a biological evolutionary process (e.g. social systems), robustness and flexibility are not necessarily guaranteed. Although this distinction is very important, we will not use it as a unit of taxonomy, as for the sake of our review both these systems deserve to be fully understood as they may contain insight that would allow us to develop useful engineering systems. In fact, although a social system, for instance, may not be behaving in a robust and adaptable fashion under certain conditions, in an engineering context, parameter conditions are fully under control, so understanding the regime in which such systems behave optimally is important. In the following, we define robustness and adaptability and clarify their interplay in the context of collective engineering systems.

In works such as those of Young *et al.* [2] and Kitano [3], robustness is referred to as the ability of the system to maintain its functionality when a system parameter changes. In collective systems, this functionality is the global behaviour that emerges from the individual behaviours, which are formulated based on the individual's opinion and the interactions with other individuals. Hence, the robustness of a collective system can be stated as the system's ability to maintain its global behaviour under the presence of perturbation, changes or failures in the individual behaviours and/or in the interaction. The impact of a failing component on the robustness of a collective system must thus be studied in terms of the other affected components and not by zooming in on the internal details of the failing component.

Adaptability in a collective system, on the other hand, can be defined as the ability of the system to shift from one collective state to another in response to a stimulus. The new state can be either better or worse than the old state. Example of collective state changes as stimuli responses are: the change in flying direction of a bird flock as a response to a predator attack; the transformation of matter from liquid state to gas state as a response to rising temperature; the selection of a new hive site by a honeybee colony as a response to unsuitability of the current nest location. Adaptability is a fundamental feature in unpredictable and dynamic environments, in which the stimuli are unknown a priori.

Robustness and adaptability may have synergistic or antagonistic interactions. In static environments in which the collective system response is not expected to change, having a high degree of adaptability may have a detrimental effect on robustness, as an adaptive reaction to noise, for example, may trigger an unneeded collective state change. On the other hand, in dynamic environments adaptability is more likely to promote robustness, as changes will most likely be triggered by environmental stimuli rather than by

the noise, thus collective state change will more likely keep the system functioning under the new environmental condition. The adaptive response to stimuli must be efficient and coherent. One way to achieve this is through a quick and wide enough propagation of information throughout the system, which again can be realized by scale-invariant interaction networks as we will discuss across this review.

In this review, we will mainly focus on scale-invariant systems that involve space-like variables (including physical positions in space, topological locations on networks, and dynamics on different physical or virtual sites). This is because space-like scale invariance can often be achieved by self-organizing systems, which are our main interest here because they can inspire distributed solutions for future engineering, design and control applications. In the following, we will describe three classes of scale-invariant systems, each associated with a different scale-invariant physical property: spatial distributions (§3), connectivity (§4) and dynamical correlations (§5).

3. Scale-invariant spatial and temporal distributions

We consider first situations where scale invariance is manifested in the structure of physical objects, in the distribution of positions in space (i.e. the physical occupation of the space) or in the signal left by the system over time. Although we will mainly focus on the scale-invariant connectivity and dynamics discussed in §§4 and 5 (since they describe *collective*, rather than *individual*, scale-invariant phenomena), for the sake of completeness, we also include below a brief description of common ways in which scale-invariant spatial distributions may emerge in nature. In contrast with the other two kinds of phenomena, these scale-invariant distributions could be generated by the action of a single individual, or by the action of multiple individuals that are not necessarily coordinated.

We start by discussing fractals, because they are a fundamental component of the study of scale-invariant structures. We then illustrate several ways in which scale-invariant structures can also be generated starting from a simple random walk. It is important to note that scale-invariant spatial patterns can also emerge in other contexts, and due to very different processes. Self-propelled microswimmers, for example, can form such patterns due to underlying fluid flows (as further discussed in §4.2). Elgeti *et al.* [4] and Wysocki *et al.* [5] have described how such fluid flows contribute directly to long-range interactions at multiple scales.

3.1. Fractal structures

Fractals are geometrical structures made of patterns that repeat themselves at all spatial or temporal scales. The study of fractals has become a broad discipline in mathematics that includes the following: how they are generated, the characterization of their geometry, examples in nature, and potential applications. These different aspects of fractals have been well reviewed in the literature, e.g. by Briggs [6], Falconer [7], Mandelbrot & Pignoni [8]. In what follows, we will describe only briefly some examples of how fractals appear in biology and other natural systems, in order to illustrate cases of both temporal and spatial scale invariance found in this context.

Prime examples of fractal time series in biology are given by Scafetta *et al.* [9], namely the physiological signals produced in response to stress and environmental changes, such as (i) beat-to-beat intervals in the human heart (or heart rate variability), (ii) human stride intervals under different conditions (e.g. different walking paces) and (iii) inter-breath intervals in patients with different conditions. Also spatial fractals were found in physiological systems by West [10] and Goldberger *et al.* [11] such as the arterial and venous trees, the branching of certain cardiac muscle bundles and the nervous system.

Some fascinating examples of fractal structures manifest themselves as morphogenic patterns in a variety of living systems. These patterns naturally emerge as these systems grow, leaving a trace on the design of the grown organism. Seashells, for example, often display geometric structures that are fractal in nature. A set of underlying mechanisms that can produce such patterns were investigated by Umulis & Othmer [12]. This work describes the spatio-temporal evolution of morphogen-mediated patterns by dividing the system into four models. The first model generates the morphogen signal, the second one redistributes the morphogen, the third one shapes the morphogen distribution and the forth one detects and transduces the corresponding signal. Umulis & Othmer [12] then show how the combination of these models leads to a scale-invariant morphogenic pattern.

Fractals have already been widely used in the analysis and engineering of artificial systems. In the time domain, examples include the study of market dynamics by Peters [13], who used a rescaled range analysis to identify fractal characterizations of market fluctuations and risk factors and to help predict future dynamics. In the space domain, the detection of fractal structures in images is an important enabler to compress data efficiently. Fractal compression has been applied by Hramov *et al.* [14] for neuro-images or by Liu *et al.* [15] for images of agricultural fields, which indeed show a high degree of repetition in their visual appearance.

3.2. Modified random walks

A set of simple mechanisms used by nature to generate scale-invariant spatial structures can be obtained by modifying the standard random walk dynamics. An example is given by self-avoiding random walks, of which a simple physical example is given by polymer systems. Polymers are large molecules composed of chains of monomers. These molecules form long strands in space that can randomly bend in different directions and can thus be described by a random walk. However, these chains cannot cross or touch themselves, so they are better characterized as self-avoiding chains or walks [16]. Such self-avoiding random walks are scale-invariant (e.g. the history of jumps as a set of temporal correlated events), and can thus be seen as a remarkable example of how simple individual interactions can lead to the emergence of a scale invariance [17].

An interesting aspect of self-avoiding random walks is that they are relatively simple mathematical objects for which several properties have been studied. For example, one of their well-understood properties is how the mean squared end-to-end distance of a walk segment R_N^2 depends on its number of steps N. As N tends to infinite, it has been shown that this distance can be approximated by equation (3.1).

$$R_N^2 \sim N^{2v}. \tag{3.1}$$

Here, v is the critical exponent that was found by Nienhuis [18] to be 3/4 for a random walk on a two-dimensional (2D) Euclidean lattice.

Another well-studied property of self-avoiding random walks is the total number C_N of distinct walks that can be performed with N steps, which is given by equation (3.2).

$$C_N \sim \mu^N N^{\gamma-1}. \tag{3.2}$$

The exponent γ was found to be 43/32 by Nienhuis [18] (also for a random walk on a two-dimensional lattice), while μ is a connectivity constant that depends on the specific structure of the lattice.

An example of a self-avoiding walk process that generates scale-invariant structures which are beneficial for survival can be found in the collective foraging of social insects. Collective foraging is the process through which groups of insects search for food. In the case of ant colonies, for example, pheromone trails could be used to generate scale-invariant search patterns. Indeed, ants typically create and reinforce search routes using chemical pheromones [19–22], which serve here as an implicit means of communication. As each ant deposits on its trail pheromones that evaporate over time, favoured routes will present a higher pheromone concentration than less used ones. It is well known that this leads to emergent phenomena, such as the selection of shortest routes, but it was also suggested by Reynolds [23] that pheromone trails can be used to avoid revisiting locations. Ants could, therefore, use pheromone trails collectively to effectively generate a self-avoiding random walk structure. This would result in a scale-invariant fractal-like search pattern with power-law distribution of path lengths, thus providing an evolutionary advantage for the colony by facilitating the collective exploration and foraging in terrains with features at all scales. An equivalent mechanism that exploits chemical odour tagging to avoid particular locations is used by phytophagous insects to control the distribution of positions where the eggs should be laid [24] and by honeybees searching for flowers that have not already been visited [25].

Another type of a random walk that does not intersect its own path is given by the *loop-erased random walk*, which is sometimes considered a simpler version of the self-avoiding random walk. A loop-erased random walk between two points is obtained by launching a simple random-walk process from the initial to the final point, and then erasing loops along the path, in order. Algorithms based on this process, such as Wilson's algorithm, are often used to create uniform spanning trees, e.g. by Aldous [26]. These trees are undirected subgraphs of a given network that include all of its nodes, contain no loops, and are chosen randomly with equal probability. As in the case of self-avoiding random walks, loop-erased random walks show their critical properties when the number of steps N tends to infinity. Guttmann & Bursill [27] have shown, for example, that in the limit the mean squared end-to-end distance on a two-dimensional Euclidean lattice is distributed following a power law with exponent $v = 4/5$ (instead of the $v = 3/4$ obtained for self-avoiding walks). The sizes of the erased loops have also been shown to follow a power-law distribution for large loops. In this limit, the probability for the perimeter of an erased loop to have length l is characterized using a power law [28].

Lévy flights are a different type of modified random-walk process that can also be used to generate scale-invariant spatial distributions [29]. They are defined as random walks in which

the direction and the length of each step are chosen randomly. In this case, scale invariance is directly imposed by picking the step length from a power-law distribution. No additional self-avoidance constraint is, therefore, required. Note that this is an example of a continuous statistical spatial invariance (in the step-length distribution) that results in a discrete pathway structure in each realization, as mentioned in §2. Lévy flights are used by a number of organisms in their search patterns. For example, soldier crabs use them in their collective foraging and some social insects, such as bees or ants, use them during their nest selection process [30–33].

4. Scale-invariant interaction networks

Scale-invariant structures in natural systems are not limited to the spatial distributions described in §3. They can likewise appear in systems in which space does not play an important role. For example, the scale-invariant property can be given by topological distance rather than by physical distance. Scale invariance is then related to the number of steps required to connect different parts of the system via inter-action links. In this case, the property of scale invariance describes the fact that, regardless of the number of parts in a given system, a similar density of interactions between them is enough to guarantee a certain level of connectivity that results in system integration and coordinated collective response. Given that the focus here is on the links between parts of the system (rather than on physical distances) these scale-invariant structures are best analysed using the tools of network theory, which we briefly review next.

One of the earliest mathematical analyses of networks was introduced in [34], in which a *theory of random networks* was developed based on the Erdös–Rényi (ER) random graph model. Random networks resulting from this model (also called *ER networks*) are constructed by considering a set of nodes that are pairwise connected with a given constant probability P_{ER}. One of the key results of this theory is that a connected network emerges suddenly once P_{ER} exceeds a critical threshold. Another important prediction is that ER networks have a narrow distribution of their node degree, where the node degree is defined in network theory as the number of links per node. When networks were analysed in the real world, however, it was discovered that they do not follow the properties of ER networks. More specifically, connected real-world networks do not emerge suddenly. Instead, they develop slowly over time, and different nodes typically have very different degrees. The differences between ER networks and real-world networks can be explained by noting that the probability of linking any two nodes does not need to be constant in real-world networks. It can instead depend on various other factors, in contrast with the assumption made by ER. A series of alternative, more realistic network growth processes have thus been proposed.

One of the most studied network growth algorithms that generates topologies that go beyond ER random networks and can often be scale-invariant, is *preferential attachment*. In this process, nodes are added to the network one by one, and newly added nodes tend to link with a higher probability to nodes that have a higher connectivity degree. This algorithm was first introduced by Yule [35] to explain the power distribution that characterizes the number of species per genus of flowering plants. It was then used by Barabási &

Albert [36] to study the growth of the World Wide Web (WWW). They verified that this process is not equivalent to that hypothesized for random networks [37].

Another well-studied network growth algorithm, which generates yet a different set of topologies that can also be scale-invariant, is the model of Watts & Strogatz [38]. As originally introduced, this algorithm consists of first laying all nodes on a regular circular formation and then connecting all first and second neighbours. This forms a regular network that is then modified by randomly selecting a new destination node for a fraction p of the links, while keeping the source node. For a range of values of p, such networks will satisfy the small-world (SW) property, that is, the topological distance between two randomly chosen nodes will grow proportionally to the logarithm of the total number of nodes.

The two network growth processes described above produce networks with specific topological properties. The preferential attachment process leads to what are known as SF networks and the Watts–Strogatz model, to SW networks. In the following two subsections, we describe these two topologies and provide real-world examples, originating from different fields, of both types of networks.

Although we limit the discussion in this review to scale-invariant structures that are directly related to *only* node degree or node distance, we should note that scale invariance can also be associated with larger network structures. For example, communities or modules (both defined as groups of nodes that are more strongly connected among themselves than to others) can organize into scale-invariant systems that involve substructures with multiple nodes. Community structures have recently played an important role in facilitating the analysis of collective behaviour in different kinds of networks. Weng *et al.* [39] have relied on community structure as their model to predict the virality of disease spreading as a property of the collective behaviour in social networks. Another example is the work of Mosleh & Heydari [40], who studied collective fair behaviour between different societies using the mode of community structures. On a microscopic scale such as neuron networks, Crossley *et al.* [41] have shown that community structure represents the underlying topology over which a set of collective cognitive behaviours emerge such as the activation of different brain regions.

As in the cases detailed below, growth algorithms that produce networks with a power-law distribution of community sizes [42] or that contain fractal-like embedded structures (resulting from either deterministic [43] or stochastic [44] processes) have also been developed. However, a detailed description of these algorithms would require a deeper discussion of the large-scale structural network properties that goes beyond the scope of this review paper. Thus, in the next subsections, we focus only on the scale invariance associated with node degree and node distance.

4.1. Networks with scale-invariant node degree
The type of networks that result from preferential attachment processes are called SF networks, defined as networks in which the degree distribution follows a power law. These can thus be viewed as networks with a scale-invariant topological property, specifically their node degree. In SF networks, most nodes thus have a low connectivity degree, but there are also a few nodes—often referred to as *hubs*—with a very high connectivity degree. SF networks often

follow the 'first mover advantage' dynamics, in which nodes that appear first in the network have the time to obtain more links (i.e. gain a higher connectivity degree) and will thus tend to become the hubs [45]. This is not always the case, however. For example, in the case of real Internet systems, Google was a relatively late-arriving search engine, but it quickly emerged as one of the most used ones: it became a hub for search requests, and many other websites started linking to the Google homepage. The rule of preferential attachment can be modified to describe such cases by making the probability of a new link to attach to a node proportional to the product of the connectivity degree and a node fitness. This node fitness describes the intrinsic ability of a given node to attract links [46,47], beyond its current connectivity properties. In the case of Google, this fitness was high from the moment the site entered the Internet, due to its very effective search algorithm.

An essential property of SF networks that often makes them particularly useful in real-world systems is their robustness to random failures. This property refers to the ability of a network to remain functional, while a fraction of its nodes or links is removed at random. Functional networks are defined here as those where the mean topological distance between nodes (i.e. the number of steps required to connect two nodes via network links) does not grow strongly when more nodes or links are removed. In the case of random networks (i.e. ER networks), random failures will typically lead to network fragmentation in a fast-speed manner. Even if only a small fraction of nodes or links is removed, the network breaks into smaller, disconnected parts and the mean distance between nodes becomes infinite. On the contrary, SF networks are very robust to random failures. In fact, studies as those of Cohen *et al.* [48] have shown that some SF networks can still function after randomly removing 99% of the nodes. The reason is intuitive: when nodes are targeted at random, it is more probably that the affected nodes will be low-connectivity nodes (because these are much more common in SF networks), which have a small effect on the overall network connectivity. However, when attackers are able to discover and disable the hubs in the collective system, the system network will rapidly disintegrate. This is thus an important flaw in the robustness of scale-invariant systems, as described by Albert *et al.* [49] and Cohen *et al.* [48]).

Given the robustness and the simplicity of the preferential attachment mechanism, we expect SF networks to appear in a broad variety of systems, ranging from molecular interaction networks to social networks. In the following, we provide a list of examples of SF networks found in nature within various disciplines.

In the context of molecular biology, a series of technological breakthroughs in recent decades have allowed us to look deeper into the inner workings of bio-molecular systems. This has resulted in large datasets that can be used to construct underlying interaction networks. Interactions in molecular systems can be physical, chemical or functional. They can be modelled as a network by defining the participating molecules (e.g. proteins, genes, etc.) as the nodes and their corresponding interactions as the links, which could be directed or undirected [50]. Although the data available for most molecular networks are incomplete, Rzhetsky & Gomez [51] have shown that the majority can be identified as SF networks. We describe some of the best-studied molecular biological networks next.

The first type of molecular networks that we consider are *metabolic networks*. These networks describe all possible chemical reactions involved in maintaining life in cells and organisms. They are constructed by associating the metabolites to nodes and their corresponding chemical reactions (involving either reactants or catalysts) to links. Jeong *et al.* [52] carried out a mathematical analysis of the metabolic networks of 43 different organisms representing all three domains of life: archaeon, bacterium and eukaryote. They found that most of them display a power-law degree distribution and are thus SF networks. They also showed a characteristic feature of metabolic networks: their *network diameter* (defined as the shortest topological distance between the two most distant nodes in a network) is similar, and relatively small, for all studied organisms. This may provide an advantage for survival, because it allows living organisms to respond efficiently to external or internal changes, i.e. to demonstrate a properly integrated collective response [53–56].

The second type of molecular networks that we consider are *protein–protein interaction* (PPI) networks. As the amount of data collected on molecular interactions increased, it became possible to also deduce the underlying PPI networks. Proteins are the main building blocks of living systems and an essential part of every cell. PPI networks represent how proteins bind to each other, and are thus represented by non-directed graphs. This binding can lead to different collective responses, including inhibition, signalling, and the production of macrostructures. PPI networks have also been found to be SF networks [51,57]. Some works have particularly focused on the PPI networks in yeast [58–60]. They have shown that yeast cells rely on a variety of signalling and regulatory mechanisms to coordinate their collective response to environmental changes such as temperature variations (often referred to as environmental stressors), and that the networks used to achieve these collective responses are SF. Furthermore, the important role of hubs has been investigated as well in these networks. He & Zhang [61], for example, have demonstrated that the PPI network hubs play an essential role for survival and reproduction. They also showed that hubs are involved in essential PPI functions with high probability, because they are by definition highly connected proteins. This implies that losing a hub protein can be lethal, which is often referred to as the centrality–lethality rule. The role of hubs has also been analysed in other SF molecular networks [62–64].

The third type of molecular networks that we consider are *gene regulatory networks*. These networks regulate gene expression, which is the process of reading genetic information to synthesize functional products (often resulting in the production of specific proteins). Gene expression involves a set of steps that include (i) transcription, (ii) RNA splicing and (iii) translation. By regulating these steps, the cell can control its functions and cell differentiation (i.e. the production of different cell types). Here, the nodes are the expressed proteins and mRNA, while the (directed) links are the reactions through which the products of one gene affect those of another. Gene regulatory networks have been shown to be approximately SF in multiple studies [65–67]. In Lee *et al.* [68], for example, the transcription regulation maps for *Saccharomyces cerevisiae* (one of the most studied species of yeast) were investigated. The degree distribution of outgoing links in the resulting networks was found to follow a power law. Note that these are directed networks because regulatory interactions are not bidirectional.

In other branches of biology, several interaction structures have also been characterized as SF networks. In neurobiology, brain connectivity networks and functional networks have been shown to have SF degree distribution [69–71] (see §4.2 for definitions of these two types of networks identified in the brain). In the context of ecology, predator–prey food webs were reported as SF networks with power-law degree distribution in several works [72–74]. These webs are defined as the networks formed by assigning a node to each species and connecting two nodes with a directed link if one of the species eats the other.

We now turn our attention to what is perhaps today the most well-known example of SF networks: human social interaction networks. Social media platforms, such as Facebook or Twitter, have become one of the main means through which we interact. They define social networks, in which nodes are individuals and the directed or undirected links between them represent their 'friendship' (e.g. on Facebook) or 'following' (e.g. on Twitter) relationships. These networks are continuously growing as new users join these platforms. At a first approximation, they tend to follow preferential attachment rules, because new users will connect with a higher probability to users that have more connections. However, Javarone & Armano [75] found other fitness values driving the linking dynamics, such as the reputation of the user or the similarity between individuals. An analysis of the different linking dynamics through which social networks grow can be found in [76].

Various online social networks have been shown to have SF properties. The large network that reflects all friendship relationships in Facebook, for example, was found to have a power-law degree distribution [77]. Likewise, other socioeconomic networks, such as Bitcoin payment transactions, were analysed and their networks were found to have SF properties [78].

A large variety of other networks related to real-world human interactions and dynamics display SF properties. We briefly describe some of these here. Most real-life social networks between individuals present a SF structure similar to that found in online social networks. One of the first examples examined from a network perspective was presented in the work of Liljeros et al. [79], which analysed the data gathered in a Swedish survey concerning the sexual behaviour of people ranging between 18 and 74 years old. In the network representation, nodes were defined as individuals that were linked if they had had sexual relations. The resulting network was found to be SF for males and females. These results were explained by considering changes in the social properties of individuals that depend on the number of current connections, all of which can be mapped to preferential attachment mechanisms. Many other social interaction networks have also been shown to be SF since this seminal study. The focus has often been on understanding how to stop the spread of viruses or other contagious agents, either biological or computer based. Dezső & Barabási [80], for example, suggested ways to focus on immunizing the hubs, which is an effective strategy because the underlying network is SF.

The real structure of a variety of human interaction networks can be deduced from available datasets. Phone numbers, for example, can be used to define networks where each node is a number and a directed link is established from the caller to the receiver each time a call is made. Aiello et al. [81] analysed these networks and showed that the outgoing and incoming link distributions follow power laws. Similarly, e-mail networks, in which each e-mail address is a node and two nodes are linked if e-mails are sent between them, also display a power-law degree distribution [82]. Furthermore, traffic networks, which can be considered as proxies for a type of human interaction networks, have been shown to be SF [83].

Cities represent a straightforward manifestation of human interaction networks. Bettencourt [84] found power laws in respect to the population size with sub-linear exponent (less than 1) for urban properties that are related to the volume occupied by city infrastructure needed to transport goods and information, as well as power laws with super-linear exponent (greater than 1) for social properties such as the number of jobs, medical services, crimes and diseases. Schläpfer et al. [85] formulate the underlying hypothesis that the sub-linear growing is related to the spatial efficiency needed for the infrastructure, whereas the super-linear exponents are associated with human interactions. A final type of real-world human interaction networks that we will describe here is given by collaboration networks. Newman [86], for example, analysed the structure of scientific collaboration networks, in which scientists are the nodes and two scientists are connected if they have authored a paper together. According to scientific databases, the resulting networks are SF and SW. Other types of collaboration networks have also been studied. For example, the IMDB database (containing information on all released movies) was used to build a network in which each node is an actor and two nodes are linked if the corresponding actors appear in the same movie. Barabási et al. [87] found this network was also SF. Similarly, a network of Marvel comic characters was studied by Alberich et al. [88], in which each character is a node and two nodes are linked if their corresponding characters appeared in the same comic book, which also resulted in an SF network.

Finally, it is important to mention that many studies claim networks with SF node degree distribution without solid statistical analysis. The technique of estimating the power-law coefficient by linear regression on a log–log histogram of the node degree in the empirical data are inadequate. Clauset et al. [89] indicate that this linear regression may lead to erroneous parameter deviations, *even* when the underlying distribution is a power law. Another critical issue while proving SF properties is the sampling procedure used. Stumpf et al. [90] proved that random subnet samples from SF networks are not themselves SF. The deviation is more pronounced with larger values of the power-law exponent, with the sampled subnets having many more nodes with relatively small node degree. This is an important finding, as many empirical datasets cover only parts of the full network, e.g. depending on the organism only 10–80% of protein interactions have been surveyed. The work on subsample scaling is an active domain of interest, e.g. a novel methodology was presented by Levina & Priesemann in early 2017 [91].

4.2. Networks with scale-invariant node distance

The type of networks that result from the Watts–Strogatz model are called SW networks. In a SW network, each node can reach any other node within a small number of hops. More specifically, the topological distance L between two random nodes is proportional to the logarithm of the total
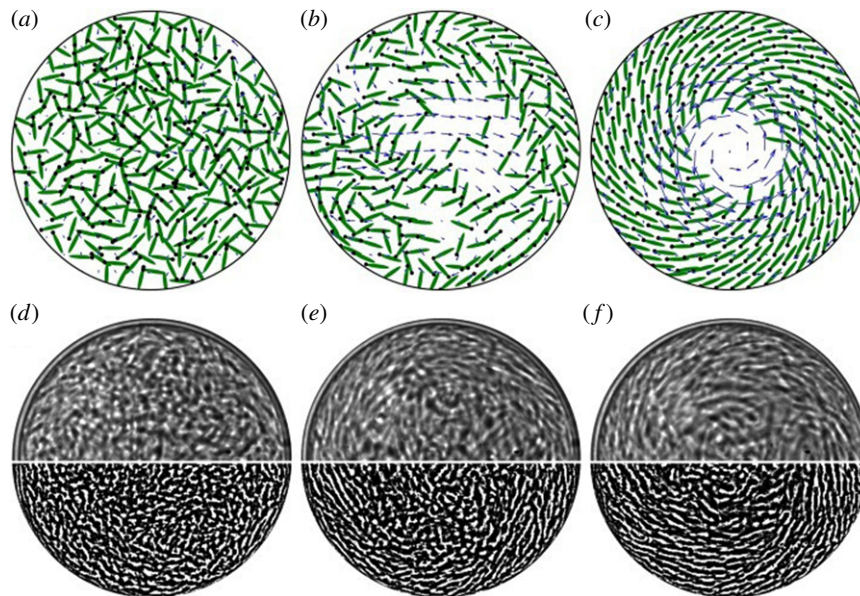
Figure 2. Self-organization of bacterial colonies in a fluid (adapted from Lushi *et al.* [94]). (*a*–*c*) Simulation snapshots. (*d*–*f*) Experimental images. In (*a*–*c*), each individual (bacteria) is represented by a green line, with a black dot indicating its heading direction, and the blue arrows show the fluid flow. The emerging structures result from long-range interactions mediated by large-scale hydrodynamic flows.

number of nodes N in the system, that is: $L \propto \log N$. Here, L can be associated with the network diameter, defined in the previous section. When considering the SW property in different types of networks, it is important to note that many real-world networks can simultaneously have SF and SW properties. In fact, many of the systems initially analysed for their SF topology were later shown to also have SW behaviour. The PPI networks discussed in the previous subsection, for example, were also studied from this perspective. Giot *et al.* [92], Watts & Strogatz [38], Yook *et al.* [93] have shown that the distance between the hubs of PPI networks is close to the typical SW network diameter. We point out, however, that the SF and SW properties are intrinsically different regarding the role of space. Indeed, whereas the SF property is purely associated to topology (physical distances are not considered), SW systems must have a combination of short-range interactions between adjacent parts in space and long-range interactions that can link any two parts of the system.

The question of how short- and long-range network connections can develop in physical space is easily answered in the context of biological systems, in which interactions (links) between components (nodes) can be of many different types. Indeed, biological interactions can be mediated by biochemical signalling, mechanical forces, symbiotic dynamics, predator–prey relations, etc., and in many cases some of these interactions are intrinsically short-range, while others are long-range. This produces a mixed topology, in which some connections are influenced by spatial constraints, while others are not, much as in the Watts–Strogatz model. A good example of this can be found in microorganisms immersed in a fluid, in which diffusive signalling interactions tend to be short-range, but hydrodynamic couplings can be long-range. This was observed by Lushi *et al.* [94] and Wioland *et al.* [95], who have shown that the reaction to stimuli in swimming bacterial colonies can result not only from the local chemical interactions, as expected, but also from long-range hydrodynamic flows (figure 2). Similar results were presented by Cisneros *et al.* [96]. A full review of the different types of short- and long-range microbial interaction, as well

as approaches for modelling them, is presented by Faust & Raes [97].

An important area where the SW properties of interaction networks have been studied in detail is neuroscience. In recent years, breakthrough brain probing technologies have allowed a deeper investigation of the dynamics of neuronal activity and synaptic connectivity (i.e. the links between neurons). Using these tools, two different types of networks have been identified: (i) the structural network that describes the static neuronal architectures and (ii) the functional network that shows the activity correlation between neurons that may or may not occur through these connections. Both types of networks have shown scale-invariant properties. This was a reasonable expectation, because neurons in the brain need to be capable of developing coherent collective responses at all scales to properly control the behaviour of an organism. In addition to the scale-invariant activity patterns that have been measured in the brain (which may or may not be related to the underlying network topology), the review by Bullmore & Sporns [69] of structural and functional brain networks based on graph theory has shown that both display not only SF topology but also SW properties. Achard & Bullmore [98] have shown that the SW feature in functional brain networks provides high efficiency (defined in terms of parallel information processing capabilities) for a relatively low connection cost, and that this efficiency decays for older age-groups, as the connection cost increases.

Another area where SW effects have been measured is Internet networks. In fact, one of the first real-world networks that were shown to be simultaneously SF and SW was the WWW network, where HTML pages are defined as the nodes and the hyperlinks between them as their connections. The SW property of the WWW is confirmed by the fact that two WWW pages are, on average, at a topological distance of only 19 hops (through hyperlinks).

Finally, various social networks have SW properties, in addition to a SF degree distribution. This is the case, for example, for the particular online social network that was studied by Wohlgemuth & Matache [99], in which the

nodes were representing Facebook groups that are linked if the groups have common users. This is also the case for Twitter [100] and in author collaboration networks [86], where nodes represent authors that are linked if they have co-authored a paper.

5. Scale-invariant dynamics

The third scale-invariant feature that we will consider in this review is scale-invariant dynamics. Systems with scale-invariant dynamics can be defined as having either local activity that displays scale-invariant correlations in space, or global activity that displays scale-invariant correlations in time. A formal example of scale-invariant dynamics in space can be described as follows. Consider an extended system in space with individual parts that evolve in time according to $f(x, t)$, where f describes a specific state at location x and time t. We say that this system has scale-invariant dynamics if the correlation function $\text{Corr}[f(x, t), f(x + z, t)]$ is a scale-invariant function of z. These spatial correlations are often related to temporal scale-invariant correlations of the dynamics of the whole system. In our example, we say that a quantity $F(t)$ that describes the system dynamics and depends on the local activity $f(x, t)$ will display such temporal scale invariance if $\text{Corr}[F(t), F(t + t')]$ is a scale-invariant function of t'.

We identify in this review three different mechanisms for generating scale-invariant dynamics: (i) the presence of an underlying scale-invariant interaction network, (ii) the development of critical dynamics with divergent correlation lengths and (iii) the selection of global collective modes. We describe next the underlying mechanisms responsible for each of these types of scale-invariant dynamics and provide examples for each.

5.1. Dynamics on scale-invariant networks

A simple way to achieve scale-invariant dynamics is through scale-invariant interactions. Simple mathematical models commonly used in statistical mechanics can develop scale-invariant dynamics when SW interactions are included. For example, the XY and coupled oscillators models have been shown to display scale-invariant dynamical correlations in their degree of global polarization and synchronization, respectively, when SW interaction topologies are considered [101–103]. Similar results have been obtained when using SF topologies in the works by Arenas *et al.* [104], Dorogovtsev [105], Kwak *et al.* [106] Moreno & Pacheco [107].

The emergence of scale-invariant dynamics as a consequence of scale-invariant interactions is not only seen in models but also in nature. Several works have shown, for example, that the gene-regulatory networks discussed in §4 display collective behaviours, such as self-sustained system-wide coherent oscillations that result from the underlying SF connectivity [108–112]. In addition, other collective behaviours demonstrated in the genetic networks, such as the functional clustering of related genes, have been found to emerge from the SF topology of gene networks [113]. In a specific example of this, it was explained by Brazhnik *et al.* [114] how coherent cell-level responses emerge from the coordinated activities of groups of genes that interact through a SF network. This work showed that hub genes were important for such responses, that cell phenotypes result from collective gene dynamics and that these dynamics strongly depend on the structure of the underlying gene regulatory network. Inoue & Kaneko [115] focused on the case of the collective adaptivity of the cells in gene expression networks and showed that such adaptive behaviour results from the interplay of positive and negative interactions between genes in a SF network.

A connection between scale-invariant interactions and scale-invariant dynamics can be found in various types of biological systems and at different scales. For instance, for groups of bacteria (which are expected to be scale-invariant because different colony sizes must still behave collectively), it is known that the structure of the underlying interaction network can play an essential role in achieving some types of collective behaviour at any scale. For example, bacteria populations use signalling to collectively coordinate and synchronize attacks against their hosts. The interaction topology underlying this signalling process has been found to be SF [116]. For organism-level responses, there is also evidence showing that integrated behaviour can be a consequence of the underlying interaction structure. Subramanian *et al.* [117], for example, studied the human immune system by describing immunity as a set of nonlinear behaviours arising from dynamic and feedback-regulated interactions between components, and when these interactions were mapped, they were shown to form SF networks.

It has been argued that the scale invariance of the human interaction topologies must produce scale-invariant collective dynamics. This has been confirmed in recent years by analysing human interaction dynamics using online data. Such dynamics include collective decision-making processes such as market choices [118], political alignments [119,120], travelling decisions [121] or news aggregation [122]. In all these cases, the emergent collective dynamics has been shown to present scale-invariant temporal behaviour, such as the self-similar, fractal-like fluctuations displayed by a variety of market indicators.

In the context of animal groups, Rosenthal *et al.* [123] studied the relevance of the underlying interaction networks in producing collective behaviour in fish schools. This behaviour must be scale invariant to remain effective regardless of the group size. In this work, Rosenthal *et al.* [123] performed a set of experiments with golden shiners (*Notemigonus crysoleucas*) to determine the actual functional interactions between individuals during evasion (a collective response). As these interactions are mainly visual, they computed the visual field of view of each individual in a series of experimental events in which initiators influenced responders to engage in evasive behaviour. They used these data to build a model that describes which individuals tend to influence the response of other fish, and then used this model to build a functional interaction network. While this network has some complex features and cannot be directly identified as a simple SF or a SW network, it does contain a significant fraction of long-range connections, because its linking probability only decays logarithmically with distance. It is, therefore, possible that the scale invariance required for collective evasive behaviour to be effective is directly related to the scale invariance of the underlying interaction network. However, as we will discuss below, in highly sophisticated biological systems such as animal groups or the brain it is hard to know if the origin of scale-invariant collective responses is in the connectivity structure or in the type of self-organized critical dynamics described in the next section.

We complete this section by considering the scale-invariant dynamics observed in the brain. It is clear that neurological activity must be more than the sum of parts and display multiple levels of collective responses [124,125]. Direct experimental observation supports this view. Indeed, a nested frequency analysis by He *et al.* [126], to unveil the spatio-temporal structure of functional brain activity, showed that the spatio-temporal structure of brain activity follows scale-invariant dynamics with power-law exponents that vary across different brain regions. A connection has also been established between exposure to scale-invariant stimuli and normal brain functioning. Indeed, an analysis carried out on the occurrence of Alzheimer's disease found that it was strongly correlated to the level of scale invariance in the degree of activity fluctuations at different ages.

Although the underlying causes of the scale-invariant behaviour observed in the brain are still unknown, it is reasonable to hypothesize that it is related to properties of the underlying interaction network between neurons. One way to test this hypothesis is to analyse the role of the hubs identified in brain networks, given their SF structure identified in §4. Achard *et al.* [127] showed that these hubs are prominent when focusing on the low-frequency (i.e. large scale) functional connectivity of the human cortex, becoming hot spots of the macroscopic states in experiments during high metabolic activity. It thus appears that hubs play an essential role in organizing local dynamics into collective responses. Hubs even seem to play a role in the emergence of cognitive functions, as suggested by Gu *et al.* [128] after studying how to control trajectories in the state space of brain functional networks. A network scale-invariant structure with hubs appears to provide the correct structure to be able to quickly reach the different collective states [129]. This allows the cortex (the part of the brain associated with higher functions such as thought and behaviour), for example, to quickly change state to achieve a diversity of functional responses, as needed [130,131]. Furthermore, at a theoretical level, simple SF models of brain connectivity have helped investigate mechanisms that may underlie various brain diseases. Batista *et al.* [132] studied the synchronization of bursting neurons that is observed in several neurological diseases (such as Parkinson's disease). Similarly, Stam [133] tried to exploit the SW and SF properties of brain networks to gain a deeper understanding of various brain disorders, using a combination of three different models to describe the brain network, as illustrated in figure 3.

The results discussed above favour the hypothesis that the brain's scale-invariant dynamics is a consequence of its scale-invariant connectivity. There is a long-standing alternative hypothesis, however, that claims that complex biological system may achieve scale invariance by placing their dynamics near a critical point. Indeed, as we discuss in the next subsection, it has been long known that physical systems near a phase transition behave as scale-invariant systems.

5.2. Criticality-driven dynamics

The theory of critical phenomena was developed in the 1970s to describe the properties of matter in a *critical system*, that is, matter close to a *phase transition* [134]. In thermodynamics, phase transitions typically describe the transition between the solid, liquid and gaseous states of matter (phases). In equilibrium and non-equilibrium statistical mechanics, they describe a broader range of changes of collective state that
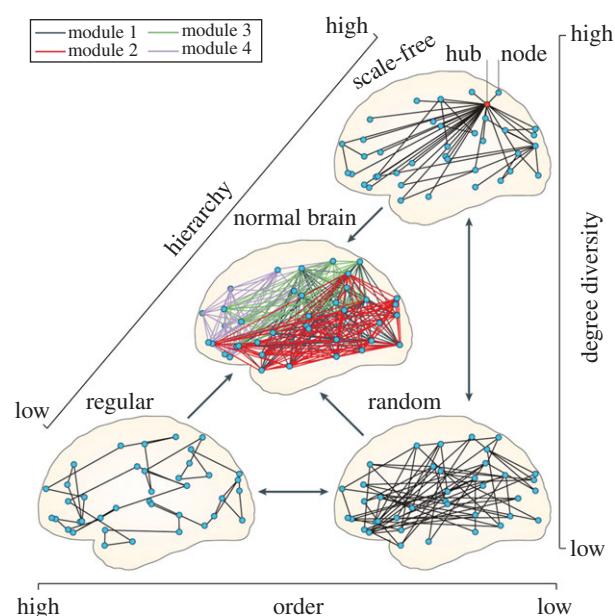

Figure 3. Organization of the brain network (adapted from Stam [133]). Its topology is described as a combination of three different types of network models: (i) a locally connected network; (ii) a random network and (iii) a scale-free network.

occur in systems composed of multiple elements. The theory of critical phenomena can be used to describe the behaviour of the system that emerges when the system is near any of these changes of state. This behaviour produces scale-invariant dynamics [134–138]. The theory of critical phenomena was originally developed in the context of standard critical phenomena (referred to here as *parameter-driven criticality*), in which the critical point is reached by tuning the system's control parameters (defined as any controllable external variable that affects the state of the system, e.g. the temperature). It was later discovered that some non-equilibrium systems can reach a critical point by relying on their own self-organizing dynamics, without requiring any external adjustment of parameters. This phenomenon is known as *self-organized criticality*. In this subsection, we will describe the underlying mechanisms that lead to scale invariance in systems that present either parameter-driven criticality or self-organized criticality, and provide examples of both.

5.2.1. Parameter-driven criticality

We begin by explaining standard *parameter-driven criticality*, and how it relates to scale invariance. Scale-invariant dynamics can be observed in a collective system near a critical point of a second-order phase transition. According to equilibrium statistical mechanics, a second-order phase transition is a change in the collective state of a system where the second derivative of the free energy is discontinuous with respect to a thermodynamic variable, but its first derivative is continuous. In second-order transitions, the phases at either side of the transition become identical as the critical point is approached. For the system to be in this unique critical phase, fluctuations must be correlated over all distances, so the correlation length becomes effectively infinite [139,140]. In non-equilibrium statistical mechanics, transitions that display a discontinuity not in the order parameter but in its derivative (as a function of changes of
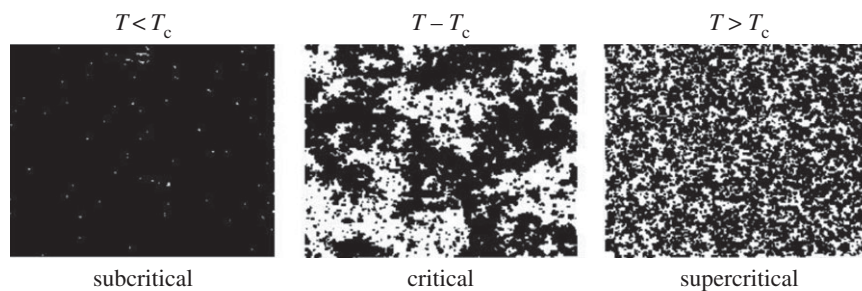
Figure 4. Two-dimensional Ising model with its two possible spin states represented as black or white dots (adapted from Chialvo [145]). The figure depicts snapshots of the spin configurations for three different regimes: (i) subcritical, where the temperature $T \ll T_c$ and the system is ordered with the same spin value throughout, (ii) critical, where $T \approx T_c$ and the distribution of the sizes of regions with the same spin value follows a power law, and (iii) supercritical, where the state of individual spins is purely random. Here, T_c is the critical temperature (see text).

the control parameter) are usually also considered second order. They inherit most properties from equilibrium systems, including their infinite correlation length. Scale invariance, therefore, naturally emerges in such critical regimes since, in finite systems, an infinite correlation length results in correlations that span a system of any size.

As a pedagogical example of parameter-driven criticality, we will focus on the model of [141], a simple abstract model originally formulated to describe ferromagnetism. The Ising model describes magnetic molecules within a metal as magnetic dipoles (referred to as *spins*) that can be in one of two states: $+1$ or -1. Spins are typically placed in a square lattice configuration where each spin interacts with its four nearest neighbours. Spins tend to align to their neighbours, that is, each spin tends to match the state of the majority of its neighbours. This alignment is hindered by noise, however, which tends to change the spin states randomly as the temperature is increased. In two dimensions, the equilibrium state of the Ising model as a function of temperature can be analytically solved. This has led to a thorough study of the two-dimensional Ising model as a simple archetypal example of a second-order phase transition controlled by temperature [142,143]. The temperature at which the transition between the disorder phase and the order phase occurs is given (for a 2D Ising model) by $T_c = Jq/K_B$, where J is a positive coefficient that represents the interaction strength between two spins, q is the number of neighbours for each spin ($q = 4$ in the classical model) and K_B is the Boltzman constant. This temperature is computed under the assumption of mean field approximation [144].

The changes of collective states associated with the Ising order–disorder phase transition can be described as follows (figure 4). When the temperature T is much higher than the critical temperature T_c (referred to as the *Curie temperature*), spins appear to be randomly oriented (i.e. they have a random $+1$ or -1 spin value). As the temperature is lowered and the phase transition is approached from above (keeping $T > T_c$), locally aligned regions emerge in the form of 'islands' (within which all spins have the same value) that are continually appearing and disappearing (figure 4). Interestingly, for $T \approx T_c$, scale-invariant features emerge: these spin islands start displaying all possible characteristic sizes and duration timescales, with both following a power-law distribution. In this critical regime, long-range correlations and large-scale behaviour thus emerge, even though spins continue to interact only with nearest neighbours. Finally, for $T \ll T_c$, most spins become aligned (they have the same spin value), which can be viewed as a form of self-organization.

Parameter-driven criticality has been applied as a controlling mechanism in the context of collective systems. For example, Lucas & Lee [146] studied binary decision-making processes based on parameter-driven criticality, where they applied an external control to influence the opinions of the individual nodes in the observed network. They showed how such networks can reach phase transitions and that these transitions are independent of the network structure. Similarly, in social networks, parameter-driven criticality was used as model to analyse different dynamic social and economic systems such as in [147], where the inner inclination of the individuals towards some political selection is defined as the order parameter. Parameter-driven criticality may represent an attractive technique to place a collective system near criticality, especially in artificial engineering systems where controlling the order parameters is feasible.

5.2.2. Self-organized criticality

We now turn our attention to the more recently discovered type of critical behaviour mentioned at the beginning of this subsection: *self-organized criticality* as described by Per Bak & Wiesenfeld [148]. Systems that display self-organized criticality follow a non-equilibrium dynamical process that drifts them spontaneously towards their critical regime, without requiring the adjustment of any control parameter. The *Abelian sandpile model*, developed by Bak, Tang and Wiesenfeld, was the first to reproduce this phenomenon. This idealized model describes a 'sandpile' formed by randomly dropping *grains* of sand that can either pile up or destabilize the pile where they fall to start an avalanche. The model can be defined as an n-dimensional cellular automaton where each cell is associated with a local pile of height h. Starting from a random initial distribution of heights, grains are added one by one at a randomly selected site with index i, so that $h_i \rightarrow h_i + 1$. If the slope formed by the cell with respect to its nearest cells is greater than a threshold value h_c, a local 'avalanche' occurs and the excess grains are moved to neighbouring cells. This avalanche can continue during multiple iterations if the local slope values of neighbouring cells then become greater than h_c. In its original formulation, the model was defined on a two-dimensional lattice ($n = 2$) with $h_c = 4$. The four excess grains were thus redistributed to the four nearest lattice cells every time a local avalanche process occurred.

Simulations of the sandpile model show that, as grains are added, the overall slope of the sandpile gradually increases and larger and larger avalanches start to occur. Eventually, the system stabilizes to a critical mean slope value. The

distribution of avalanche sizes and of avalanche lifetimes both follow a power law, and therefore display no characteristic scale. This corresponds to a self-organized critical state that can be understood as follows. As grains are added, the system drives itself to the highest slope it can achieve until it reaches the edge of a chaotic state, which corresponds here to an avalanche. If more grains are added after this slope is reached, the chaotic regime will be briefly explored as the system quickly relaxes back to a static sandpile state. The system is thus repeatedly pushing against the chaotic phase and falling back to a stable phase, thus spontaneously placing itself in a collective state that is in a critical regime between two phases. As in the parameter-driven criticality case, all characteristic scales are lost in this regime and the system displays scale-invariant collective dynamics [149–151].

Another well-known example of self-organized criticality is given by the forest fire model of Drossel & Schwabl [152]. In this model, a forest is described by a square lattice in which each cell can be occupied or not by a single tree. The mean fraction of occupied cells (i.e. the tree density) is defined at time t by a function $P(t)$, which fluctuates as some trees multiply while others burn. The model is updated using the following rules: (i) a cell becomes empty if its corresponding tree burns; (ii) a tree burns if at least one of its nearest neighbours is burning; (iii) a tree burns spontaneously at any occupied cell, with a given fixed probability, even if no neighbour is burning; and (iv) a tree grows spontaneously at any empty cell with a given probability. As the model evolves, $P(t)$ grows until a fire starts. The 'chaotic' phase is then reached and trees start burning, which reduces $P(t)$ until the system is brought back to a stable state where it starts growing again. The system thus spontaneously self-organizes by driving itself to the edge of the chaotic phase until $P(t)$ stabilizes at a critical level P_c, which corresponds to the percolation threshold. As in the sandpile case, Pagnutti et al. [153] revealed that the system then displays two scale-invariant properties: the distribution of gap sizes between trees and the distribution of fire lifetimes. Turcotte [154] and Boer et al. [155] have verified the power laws of both properties in numerical simulations and using real data from North American and Australian forest fires.

In addition to the models introduced above, self-organized criticality has been used to describe the potential underlying mechanisms of a number of complex collective behaviours that gradually accumulate energy later released in catastrophic events with no predetermined scale. Examples are found for earthquakes in the works of Olami et al. [156] and Sornette & Sornette [157], for solar flares in the work of Boffetta et al. [158], and in the work of Hergarten & Neugebauer [159] for landslides. These systems have demonstrated various scale-invariant features. For example, both the earthquake sizes [160] and the frequency of aftershocks [161,162] can be described using power-law statistical distributions. Similarly, the frequency and energy distributions of solar flares also follow power laws as shown in the studies of Aschwanden et al. [163], Baiesi et al. [164], Lu et al. [165].

Another important ecological example, for which self-organized criticality was used to interpret the underlying dynamics, is population growth and extinction. Markov chains represent a popular stochastic technique to model the lifetime of species, see e.g. Black & McKane [166]. The extinction times predicted by Markov chains approach asymptotically an exponential distribution, which can be explained through species not adapting quickly enough to the continuously changing environment (an effect that was coined by Chr [167] as the Red-Queen effect). This leads to the extinction probability being independent of time and hence the exponential distribution emerges. However, it was revealed that exponential distributions are not always providing the best fitting to the empirical data obtained. In several works such as Drake [168], Sneppen et al. [169], Sole & Bascompte [170], instead power-law distributions were found to offer the best fitting for lifetime data in large populations. In such cases, the ecosystem was observed by Pigolotti et al. [171] as a collective system of interacting species the dynamics of which converge near to a critical point. The extinction of specific species by placing the ecosystem near criticality is not the result, in this case, of a response to an external parameter, but as a response to the interactions and competition with the other species. Such an evolutionary behaviour may not advertise robustness in the specific species that became extinct. The robustness here is to be observed on a higher level, i.e. the robustness of the whole ecosystem as a result of being adaptive to the ever-changing environment.

As mentioned above, in many complex biological systems it is unclear if the emergence of scale-invariant dynamics is a consequence of an underlying scale-invariant interaction network or of being in a critical regime. In the previously discussed context of brain dynamics, for example, the observation of SF correlations in brain activity has led to the growing popularity of a hypothesis that claims that the brain must be near criticality [172,173]. Researchers have even discovered neuronal avalanches where the fraction of active neurons involved follows a power-law distribution, just as in a sandpile model. Furthermore, by establishing analogies with the Ising model, other groups have argued that certain neuronal networks must operate near a phase transition [145,174], because systems in this regime have better information processing capabilities and can more easily switch between different states of collective activity [175]. However, given that a similar behaviour can be achieved by having interactions that follow scale-invariant topologies, it is still unclear to what extent the observed dynamics results from the brain self-tuning into a critical state or from an underlying scale-invariant interaction network.

To end this section, we will discuss another system in which the origin of the observed scale-invariant dynamics is unclear: animal collective motion. In recent years, significant efforts have been made to understand the underlying mechanisms used by different animal groups to achieve collective motion. However, it is still unclear how large groups can maintain consensus in their heading direction, despite the presence of noise and what appear to be only local interactions. These systems are often described using a minimal flocking model, first described by Vicsek et al. [176], in which a set of self-propelled point particles advance at a fixed speed and tend to align their heading direction with other particles within an interaction range. The Vicsek model has been extended in multiple ways to describe a variety of collective motion systems [177–181]. Animal groups are expected to have scale-invariant behaviour, because they must display coherent collective dynamics regardless of the group size. This behaviour has been observed experimentally. Fish schools, for example, are known to react to
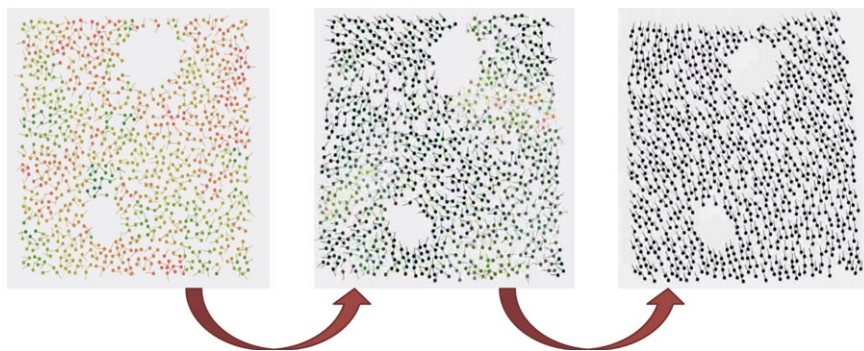
Figure 5. A self-organized flocking process that starts in a disordered state (left) and eventually converges to a parallel motion state (adapted from Ferrante *et al.* [195]). This system was shown to exhibit scale-free correlations due to the propagation of collective modes in the work by Huepe *et al.* [194].

external perturbations (such as predator sounds or an artificial predator fish) as a coherent unit [182–184]. Furthermore, Cavagna *et al.* [185] measured the three-dimensional trajectory of every bird in multiple starling flocks, and analysed their speed and velocity fluctuations (after subtracting the motion of the centre of mass), showing that the correlation length of these fluctuations is linearly proportional to the system size and, therefore, scale-invariant. However, the Vicsek model does not display such scale-invariant behaviour, unless the noise level is tuned to achieve a critical regime. This has led Attanasi *et al.* [186], Bialek *et al.* [187], Cavagna *et al.* [185] to claim that starling flocks must be in a critical regime, which would explain their scale-invariant correlations. But there could be other underlying causes of scale invariance, such as the long-range visual interactions identified in the experiments with golden shiners described in the previous subsection. We will describe in the next subsection yet another alternative cause for this behaviour, based on mode dynamics. Finally, we note that other studies, e.g. by Chen *et al.* [188], have also shown scale-invariant correlations in the dynamics of the collective motion of microscopic biological systems such as bacteria. Nevertheless, it is also unclear if these result from criticality or if they are the consequence of long-range (scale-invariant) interactions, which in this case could result from the type of hydrodynamic flows discussed in §4.2.

5.3. Collective mode dynamics

The final mechanism for achieving scale-invariant dynamics that we will discuss in this review is related to the presence of collective modes that can propagate with almost no resistance throughout the system, which can lead to persistent scale-invariant behaviour when combined with active matter dynamics.

It was discovered in the context of condensed matter and quantum field theory that infinite correlations can spontaneously emerge in the dynamics of systems that are not in a critical regime if they have gone through the spontaneous breaking of a continuous symmetry. This occurs when equations that describe a symmetrical state produce asymmetrical solutions, which leads to a degenerate ground state that poses no resistance when drifting from one of these solutions to others. An example is given by a group of vectors that tend to align due to the interaction between them (as in the XY-model for ferromagnetic materials). The alignment can be in any arbitrary direction in space. The symmetry breaking occurs when a specific direction is picked, but a simultaneous change in the pointing direction of all vectors costs no energy (there is no resistance). The excitation that corresponds to this change is referred to as a Nambu–Goldstone mode, and in the context of quantum field theory it is identified with a massless particle; the Nambu–Goldstone boson Goldstone [189], Goldstone *et al.* [190], Leader & Predazzi [191], Nambu [192].

The possibility of measuring scale-invariant correlations which result from dynamics resembling that of massless Nambu–Goldstone modes has been recently considered in *active matter* systems. These are systems in which individual components inject mechanical energy at a small scale, which must self-organize to achieve work at larger scales. They include the animal groups displaying collective motion discussed in the previous subsection, but also include other collective systems with self-driven components, such as bacterial colonies or skin tissue. Because of the continuous injection of energy at small scales, massless (or low-mass) modes, which typically span large spatial scales, correspond to system-wide coherent motion that follows scale-invariant dynamics. This potential mechanism for scale-invariant dynamics was pointed out by Cavagna *et al.* [185] as an alternative explanation (that does not require a critical regime) for the scale-invariant correlations observed in the orientation (flight angle) fluctuations of bird flocks. Indeed, since the rotational symmetry has been spontaneously broken in any group of birds that align their velocities, bird rotation costs no energy and the massless Nambu–Goldstone mode of rotational perturbation results in scale-invariant correlations of the orientation [193].

Some works have considered active matter systems where scale-invariant dynamics in the angular *and* speed fluctuations can emerge from massless or low-mass modes. Huepe *et al.* [194], for example, postulate this mechanism as the source of the SF correlations measured for speed fluctuations. They proposed a simple position-based model that describes an idealized active elastic system in which large-scale collective oscillations (corresponding here to the low-mass modes) dominate the dynamics [195] (see figure 5 for an example of possible dynamics induced by this system). They then showed in numerical simulations that the presence of these collective oscillations of the fundamental elastic modes produces scale-invariant correlations of the angular and speed fluctuations in active systems. The presence of scale-invariant correlations in bird flocks was also studied through simulations by Hemelrijk & Hildenbrandt [196]. In this paper, Hemelrijk & Hildenbrandt [196] used a detailed model of the motion rules of starlings and found that SF correlations were observed even when far from any

critical point. Their work did not focus on the causes of such correlations, but studied instead how correlation lengths change as a function of the number of influential neighbours and of individual speed control. Finally, a fundamental theoretical argument for the presence of scale-invariant dynamical correlations in collective motion systems with position-based interactions was given by Melfo [193]. Nambu–Goldstone bosons are therefore expected to also appear in speed-perturbations (associated with translational symmetry), and not only in angular perturbations. This can thus lead to the emergence of scale-invariant dynamical correlations that include speed perturbations [197].

6. Engineering scale-free systems

From an evolutionary perspective, strong system integration is ubiquitous in natural systems at all scales, because it improves the survival probability by enhancing adaptivity and robustness to challenges and stimuli at different scales. By understanding the underlying mechanisms that lead to these beneficial properties, we will be able to use them through bioinspiration and biomimetics in artificial systems. In this section, we will discuss the type of engineered systems in which scale invariance could be beneficial, and how the three different scale-invariant features identified in this article (spatial, connectivity and dynamics) could be implemented.

The first type of scale-invariant systems presented in this paper are those that display scale-invariant spatial features such as fractals or scale-invariant structures and trajectories. Scale-invariant spatial features can have many different potential applications in artificial systems. We describe here only a few. A prominent example can be found in the field of morphogenetic engineering [198], which studies the systems endowed with information that can create autonomous morphologies and functions. This field has already led to successful applications, such as demonstrations showing that self-organizing robot swarms can build different morphologies, each useful to tackle a different environmental situation [199–201]. Despite their success, none of these works have achieved scale-invariant structures so far. A different possible application, which can benefit from scale-invariant spatial features, is collective construction, whereby different materials rather than robots are used to build structures such as defense barriers, nests and bridges. One of the challenges in this task comes from the need to perfectly position and align construction materials to the partially built structure and to have materials and hardware that facilitate this task [202]. More recently, a few studies focused on using more amorphous materials in order to build structures the shape of which depend on the self-organized process leading to their construction [203]. We believe this is the right approach that may lead to the same type of scale-invariant structures observed in nature. Two final examples of scale-invariant spatial features encountered in nature with direct potential applications are given by the fractal-shaped pheromone trails and by the power-law-distributed random-walk trajectories, both used to enhance exploration and foraging. Although depositing pheromone trails can be challenging for artificial artefacts (despite some attempts that have already been made with robots, see [204,205]), the pheromone concept can be used to build scale-invariant robot chains to facilitate exploration (so far, only non-scale-invariant chains have

been considered, see [206]). Additionally, some attempts to implement power-law distributed random walks in robot swarms have already been made. Dimidov et al. [207] implemented Lévy-flight distributed random walks and compared them with traditional random walks (i.e. non-power-law distributed) considered in swarm robotics, showing that Lévy flights and a novel random-walk method they proposed (also power-law distributed) achieved better performance in terms of resource localization and signalling. This appears to be an interesting research direction that needs to be further pursued.

The second mechanism identified in this review paper for achieving scale-invariant integration is the implementation of interaction networks that are either SF or SW. As discussed in §4, SF networks have the advantage of being strongly robust to random failures, i.e. failures that can occur to any component of the collective system with equal probability. On the other hand, SW properties enhance collective response, since the small network diameter allows for the rapid transmission of information throughout the system. Quick and coherent system responses can be crucial for survival. From an engineering perspective, an advantage of SF networks (which often also display SW properties) is that they can be easily implemented, at least, in the static topology of artificial systems that have no spatial restrictions. A simple example is given by the possibility of setting up SF wireless sensor networks (WSNs), following a simple algorithm such as preferential attachment. WSNs consist of a large number of nodes with limited sensing range that are cooperating to achieve a global perception of the environment in which they are deployed. Tasks performed by WSNs are routing [208], chaining [209], aggregation of sensory data, and analysis of correlation in the data, among others. The latter example, analysing data correlations, can be helpful in avoiding redundant transmission and in reducing node energy consumption, one of the main challenges in the field. Some of these tasks have been optimized by exploiting the properties of SF and SW topologies [210,211]. SF topologies can also be used to reduce energy consumption. Zhu et al. [212], for example, propose an energy-efficient model for WSNs that constructs the network, according to the node-degree and the fitness value of the remaining energy of the node. The obtained topology is SF, which is more tolerant to random node failures and demonstrates better energy savings. Similarly, Jian et al. [213] introduced an energy-aware model based on SF topology to balance the network connectivity and consequently the consumption of energy. Another example of the use of SF topology for energy-saving purposes is given by Wang et al. [214], who proposed a new method referred to as the 'flow-aware SF' model to balance energy consumption during a network operation phase. Jian et al. [215] analysed the link between the logical topology and the physical topology of WSNs and proposed a SF logical topology that helps optimize connectivity and lifetime at the physical topology. Finally, Zhao et al. [216] exploited SF topology to design a WSN, on a three-dimensional terrain, that is tolerant to random failures.

In addition to WSNs, SF topologies could be leveraged for other potential applications. Besides increased robustness, they could be used to implement collective systems on larger scales using modular units placed at distant locations. An example is given by robot swarms distributed over the planet, whereby robots in the same geographical area would be interconnected through local interactions, while hubs in each location are connected to hubs in distant locations (i.e. via the Internet). Furthermore, given our discussion in §4 regarding the role of

SF and SW connectivities in the brain, another potential application of these types of connectivity could be the realization of collective systems able to exhibit swarm cognition [33], that is, capable of achieving cognitive tasks (discrimination, decision making, planning, etc.) through distributed self-organized processes.

Implementing SF or SW interaction networks is probably the simplest way to achieve scale-invariant properties. The main requirement for this, however, is to have *controllable topology*, which is not always the case. Straightforward mechanisms for achieving SF node degree distributions such as preferential attachment are easily implemented in systems in which all components can be easily connected, but have not yet been extended to systems in which spatial distances play an important role, such as moving systems, where agents are continuously entering and leaving the communication range of other agents. Examples of engineered systems where SF topology would be hard to achieve include Mobile Ad-Hoc Networks (MANETs) [217] (that is, WSNs equipped with mobility) and swarm robotics [218–221]. Within swarm robotics, an interesting research direction could be to use virtual potential functions [222] that allow the control of robot formations to achieve SF topologies. Another interesting direction could be to create hybrid swarms in which a small proportion of the robots are equipped with long-range interactions and can thus operate as hubs, connecting portions of the swarm that are far from each other.

The final type of scale-invariant property considered in this article was SF dynamics. In natural systems that display this property, effective collective responses to environmental stimuli is the main advantage, as SF correlations effectively allow the information perceived locally to reach other parts of the collective system at any scale. This is important in many natural systems such as fish schools or other animal groups. The example of animal groups can inspire a few engineering applications in the fields of WSNs and swarm robotics. In WSNs, SF dynamics can enable locally sensed information (e.g. the presence of an intruder in surveillance systems, or of survival in disaster recovery) to spread effectively throughout the network. Analogously, it could be used in swarm robotics to effectively identify and propagate information perceived locally by only a few members of the swarms (e.g. the location where a specific signal was identified locally or the location of a resource that requires the deployment of multiple robots).

The implementation of scale-invariant dynamics in artificial systems could benefit from the tools derived from statistical physics. We know, for example, that scale invariance emerges naturally in critical regimes and when Nambu–Goldstone modes are present. If we understood how to design local dynamics and interactions that develop these features, the implementation of self-organized scale-invariant systems would be greatly simplified. The decentralized motion control swarm robotic algorithm implemented experimentally by Ferrante *et al.* [223], for example, appears to robustly display scale-invariant correlations in its dynamics despite being far from a critical regime. There are still almost no efforts in this direction, however, and more research is thus needed.

7. Conclusion

We have reviewed in this paper examples from different fields of science that show how natural systems achieve scale-invariant collective behaviour characterized by a high degree of system-level integration. We analysed the main mechanisms that lead to natural systems that exhibit scale invariance, while providing various examples of scale-invariant properties observed in different biological systems at the molecular, cellular and organism levels, as well as in neuroscience and social networks.

When designing artificial collective systems, we may need them to display sensitivity and an effective collective reaction to stimuli as a single unit, regardless of the scale of the system or of the stimuli. This can be achieved by implementing scale-invariant features in our engineered systems. The challenge is how to achieve this goal in a decentralized and self-organized way. As we have discussed here, this challenge has been solved by many systems in the natural world. We thus hope that the examples discussed in this review paper will help inspire the design of artificial systems that display beneficial scale-invariant properties.

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