REVIEW

Dual-phase evolution in complex adaptive systems

Greg Paperin*, David G. Green and Suzanne Sadedin
Centre for Research in Intelligent Systems, Monash University, Clayton 3800, Australia

Understanding the origins of complexity is a key challenge in many sciences. Although networks are known to underlie most systems, showing how they contribute to well-known phenomena remains an issue. Here, we show that recurrent phase transitions in network connectivity underlie emergent phenomena in many systems. We identify properties that are typical of systems in different connectivity phases, as well as characteristics commonly associated with the phase transitions. We synthesize these common features into a common framework, which we term dual-phase evolution (DPE). Using this framework, we review the literature from several disciplines to show that recurrent connectivity phase transitions underlie the complex properties of many biological, physical and human systems. We argue that the DPE framework helps to explain many complex phenomena, including perpetual novelty, modularity, scale-free networks and criticality. Our review concludes with a discussion of the way DPE relates to other frameworks, in particular, self-organized criticality and the adaptive cycle.

Keywords: complex systems; dual-phase evolution; phase transition; network theory; connectivity

1. INTRODUCTION

A central problem in research areas as diverse as physics, biology, sociology and computer science is to understand how large-scale properties, behaviour and organization emerge within complex systems. The prevalence of such problems has driven the growth of complexity theory, a field that aims to draw together ideas from many different disciplines into a coherent and unified methodology [1,2]. Complexity theory has revealed many deep similarities between superficially unrelated systems and processes. For example, epidemics, wildfires and nuclear fission differ enormously in terms of the objects involved, yet they can all be usefully treated as instances of percolation [3,4].

In this review, we argue that recurrent phase changes in the interaction density of system components (i.e. density of underlying interaction networks) constitute a general mechanism for self-organization in biological complex adaptive systems (CAS), as well as in some non-living complex systems. As a consequence, we propose a common framework useful for reasoning about complexity. We term this framework dual-phase evolution (DPE). We then survey a body of literature, drawn from several fields, about the role of networks and network connectivity in complex systems. We show that the DPE framework identifies the common features of the reviewed phenomena, and highlights a common causal process.

This paper is organized as follows.

— We begin by briefly discussing the role of network theory in complexity research (§2). This includes how networks can be used for modelling system components and their interactions, as well as system states and dynamics. In §§ 2.3 and 2.4 we discuss the implications of connectivity phase transitions and provide an overview of the key topological structures found in networks.

— Section 3 presents an interpretation context for the literature reviewed in the latter sections. We identify the mechanisms that are common to the reviewed systems and draw our conclusions together into the DPE framework.

— In §4, we survey systems in which connectivity phase changes contribute to the emergence of complex system properties. Beginning with physical complex systems, we examine biological and socio-economic systems, as well as mathematical and computational systems.

— In §5 we describe some applications of the DPE framework, including generative models for scale-free and modular networks and DPE models for the origins of diversity and perpetual novelty in biological ecosystems.
Finally, in §6, we relate the ideas discussed in this paper to two other frameworks for reasoning about complex systems—self-organized criticality (SOC) and the adaptive cycle (AC).

2. BACKGROUND: NETWORKS IN COMPLEX SYSTEMS

Complex systems are composed of many interacting components and display behaviour that is difficult to explain through an analysis of the systems’ constituent parts [5]. Such behaviour is called emergent [6]. CAS are complex systems that have the capacity to adapt to their environment through an evolution-like process [7,8]. Green [9] showed that complex systems are isomorphic to networks (nodes linked by edges). Many authors argue that understanding network properties is crucial to developing general, cross-disciplinary theories of complexity and that many complex properties emerge from the structure of the networks and not from the individual system components [9–11]. Detailed accounts of network theory, including basic terminology and mathematical models, as well as the wider role of network theory in complexity research, can be found in review papers (e.g. [12–14]), and in texts on graph theory (e.g. [15,16]). Here we primarily concentrate on the role of network connectivity in complex systems.

2.1. Modelling system composition

The primary objects of our study are interaction networks that underlie complex systems. Nodes (vertices) in such networks represent system components, and links (edges) represent pair-wise interactions between the components. Broadcast-style interactions can be represented as several pair-wise interactions.

We refer to interactions as ‘local’ or ‘global’. Local interactions are interactions between nodes within a defined neighbourhood. There are various possible ways of defining a neighbourhood relation for nodes, including the nodes’ spatial location in the real world, node similarity or affiliation to a common sub-system. Many systems contain several distinct networks and the scope of some interactions can be described in terms of another network. For example, in an online social network, where nodes represent individuals and edges represent friendship ties, an email communication between two friends can be seen as a local interaction and an email between unconnected participants without common friends can be seen as a distant or global interaction. In this sense, we use the term global interactions for pair-wise interactions between any nodes in the network, which do not belong to the same neighbourhood.

2.2. Modelling system dynamics

State spaces of dynamic systems form directed networks in which the states are nodes and the transitions define edges [9]. Thus, system dynamics can be modelled in terms of state-transition networks, allowing the application of graph-theoretical analysis techniques. Sparse connectivity of state-transition networks often implies simple behaviour, while richly connected state-transition networks are associated with chaotic behaviour. A connectivity phase change between well connected and poorly connected state-transition networks often marks a transition between simple and chaotic behaviour, a region sometimes termed edge of chaos [17,18].

The concept of state-transition networks is related to two other widely used concepts: stability landscapes and fitness landscapes. Fitness landscapes, derived from evolutionary biology, map possible system states to a measure of success under competitive selection. Entities evolving under selection ‘climb’ fitness peaks and ‘avoid’ fitness valleys [19,20]. Conversely, stability landscapes map system states to relative stability, with attractors represented as sinks and ridges representing thresholds between attractor basins. Systems ‘fall’ towards the nearest attractor, and are resilient to changes until pushed across a ridge to a different attractor [21]. Thus, the fitness landscape represents an inverted stability landscape for systems under selection.

State-transition networks represent system dynamics directly rather than modelling fitness/stability topology. However, the three concepts are closely related because the dynamics of systems are directly influenced by their fitness/stability landscapes. Systems located close to an attractor (fitness peak) reside in areas with likely transitions to states closer to the attractor and fewer or less probable transitions away from the attractor. Crossing stability landscape ridges (fitness valleys) amounts to traversing from one region of a state network into another region where transition probabilities are biased towards a different attractor (fitness peak).

It is important to note that real state spaces are highly dynamic and multi-dimensional, and the metaphor of a fixed three-dimensional structure is often deceptive. For instance, in high-dimensional fitness landscapes, genotypes of similar fitness are often connected in networks and are not separated by fitness valleys as suggested by intuition obtained in three dimensions [19,22]. State-transition networks explicitly incorporate probabilistic system dynamics and high-dimensional state spaces.

2.3. Phase changes and connectivity

Perhaps the most important consequence of the universality of networks is the connectivity avalanche. Erdős & Rényi [23] showed that random additions of edges to a graph lead to a critical transition from disconnected to largely connected dynamics (figure 1). This mechanism underlies phase changes in many systems, such as freezing of water, crystallization and nuclear chain reactions [24]. At the critical threshold point, the probability of a percolation process spreading throughout the entire system (e.g. of a disease spreading throughout a population) undergoes an abrupt change from near 0 to near 1 (for sufficiently large systems). Therefore, connectivity patterns of interaction networks can determine whether stimuli propagate locally or globally in the system. When the connectivity of networks falls near the percolation threshold, propagation of stimuli is highly stochastic [3].
2.4. Topological properties of networks

Topological network structures (patterns of connections among nodes) play important roles in systems and can influence their behaviour. Such patterns include circuits, trees, modules and clusters, scale-free networks, and small-world structures.

Circuits produce feedbacks (both positive and negative). Trees (networks containing no circuits) are associated with hierarchies, encapsulation and modularity. Modular network structures facilitate several properties found in many complex systems, such as stability [25], robustness [26,27], evolvability and capacity to adapt [28,29] by promoting reusability of parts and constraining feedbacks. For this reason, modular approaches are common in problem-solving. Some mechanisms that may produce modularity in certain biological networks have been proposed [28,30]; however, the generic mechanisms involved are still poorly understood (however, see §5.3). Scale-free networks (see §5.2) are those in which the distribution of node degrees (number of edges connected to a node) follows a power law [31–33], and small-world networks consist of predominantly local connections and a few non-local cross-connections [34].

3. THE DUAL-PHASE EVOLUTION FRAMEWORK

In this section, we provide an interpretation framework for the literature reviewed in this paper. We highlight the common underlying network processes, and lay out how these processes affect system dynamics.

As we saw in §2, networks are inherent in all complex systems, and patterns and processes that occur within the underlying networks play a fundamental role in the emergence of system-wide properties. The literature reviewed in §4 shows that phase changes occur in many kinds of complex system. A common thread through the reviewed literature is that key system properties emerge owing to transitions between well-connected and poorly connected phases in underlying networks.

3.1. Well-connected phase

In the well-connected phase, typified by high edge density and short path lengths, interactions can occur between most system components. Thus, the well-connected phase is typified by global interactions in the sense of §2.1. As processes can spread rapidly in well-connected networks (see §2, in particular, network theory reviews cited there), such systems often exhibit little local variation, but may be highly variable (see [30] for a discussion of variation versus variability). Dense interactions among control variables tend to stabilize systems, but also lead to increased coupling thereby reducing robustness to external perturbations (see also §6.2). This makes highly connected systems hard to predict in their responses to external stimuli. Selection in well-connected systems acts globally and can promote attractor stability: local perturbations, if advantageous, spread rapidly, generating uniformity. Consequently, state space exploration is reduced and systems converge towards the nearest basin of attraction.
3.2. Poorly connected phase

In the poorly connected (or disconnected) phase, edge density is low, path lengths are long and the network typically consists of several sub-networks. Interactions mainly occur locally or only within sub-networks (see local interactions defined in §2.1). Propagation of stimuli is thus locally constrained (§2). Poorly connected systems typically exhibit strong local variation, but little large-scale variability. Their decoupled dynamics imply that large-scale responses to external stimuli can be described in terms of sub-systems and are thus easier to predict. In CAS, evolutionary competition in poorly connected systems is locally constrained, permitting the exploration of alternative adaptation strategies and directional selection towards novel niches.

DPE occurs when networks that dominate the dynamics of an evolving system repeatedly switch between well-connected and poorly connected phases (figure 2).

Here we argue that DPE is common to adaptive as well as to other complex systems that exhibit self-organization (e.g. physical systems discussed in §4.1). The term DPE thus implies a general process of complex development, rather than evolution in a strict biological sense. DPE-driven self-organization may account for several properties widely observed in complex systems, including sustained diversity, perpetual novelty, modularity and scale-free topologies (see §5).

An important consideration when linking network phases to system dynamics is that different networks within a single natural system may be in different connectivity phases. For example, a cell can be viewed as an ensemble of various networks, e.g. protein–protein, protein–DNA and protein–metabolite networks [10]. Specific system properties may be generated by single networks or by feedbacks between multiple networks.

For instance, at least two major networks can be identified for plant evolution in landscapes [35]: one is a network of reproductive interactions between patches of interbreeding plants. It facilitates gene flow and acts against adaptive radiation. The second is a network of unoccupied patches. An increased presence of such patches disrupts gene flow and aids percolation by newcomer species by increasing the connectivity of their invasion paths. The impact of high- and low-connectivity phases on system dynamics is essentially opposite between these two networks. Crucially however, from either perspective, connectivity phase transitions are linked to changes in dominant system dynamics.

Network connectivity density does not always need to cross the critical percolation threshold in order to flip a system between well-connected and poorly connected regimes. For instance, some connected networks may still be sparse and exhibit long path lengths between nodes. Thus, stimuli may lose their significance by the time they are transmitted via a series of interactions, leading to poorly connected dynamics. An increase in connectivity can reduce path lengths and cause a transition to well-connected dynamics. Examples can be found in collaborative social groups. Although information can always be transferred between members via common collaborators, this is often perceived as inefficient, and projects are usually organized as a succession of work in small groups (sparse interactions) and larger meetings (dense interactions).

While topological properties of underlying interaction networks can drive system dynamics, the topologies of state-transition networks are an emergent property of the system (§2.2). DPE phases of local interactions and enhanced evolutionary exploration often correspond to phases of dense connectivity in state networks with increased transition possibilities between attractor basins.

4. CONNECTIVITY PHASE CHANGES IN COMPLEX SYSTEMS

Network connectivity governs the dynamics of many systems and recurrent phase transitions in connectivity are common. As a result, we argue that DPE plays a part in self-organization within many systems. Below, we examine a wide range of complex systems and show that recurrent phase transitions, of the kind postulated by DPE, facilitate the emergence of key system properties. The role of DPE in some of the reviewed systems is summarized in table 1.

4.1. Non-living systems

DPE phase changes are a key factor for self-organization in physical systems across many scales. Here, we discuss examples spanning geomorphological processes in landscapes through to star formation in galaxies back to DPE processes on the molecular level employed in manufacturing.

Recent changes in the connectivity of underlying networks play an important role in landscape geomorphology [36]. Connectivity phases influence the size and location of catchment areas [37], as well as composition patterns of sediment deposits [36], and are crucial to understanding past climates and landscape dynamics [37,38]. Persistence of features shaped by these changing connectivity patterns provides a form of memory in the system (stigmergy). For instance, repeated flips in connectivity between water bodies drive the formation of many typical geographical features within river basins. Backswamps are moist, swampy areas of a floodplain located away from a major stream [39]. They are formed and sustained through recurrent connections to the main channel occurring during floods. Heavier sediment particles are dropped by the flood water close to the main channel and form natural levees [40], while fine alluvium is carried a greater distance. The fine material can hold significant amounts of water and drains slowly creating wetland areas. After the flood retreats, the alluvium becomes denser and swamps can develop. Backswamps can increase in size and volume through repeated restoring and breaking of water connectivity to the main channel by subsequent floods [41,42].

Recurrent water connectivity also affects the morphology of braided river channels [43,44]. These initially form when a stream is divided into several smaller channels by accumulation of in-channel deposits. When water levels rise, for instance through seasonal
discharge, the braids can become reconnected. When water levels fall subsequently, the stream often settles on a new, more efficient, layout of channel braids. Such repeated transitions of between-channel connectivity contribute to continual morphological diversity within floodplains [39,41–44].

On larger scales, geomorphological landscape connectivity describes the extent to which sediments are transported between distant sites by erosive processes such as streams and flows [45]. This form of landscape connectivity crucially influences landscape morphology [36,37] and biophysical fluxes [45]; it affects the transmission of perturbation responses through catchments and is thus a key factor for landscape sensitivity to disturbances [37,38,45].

Several factors can impede or facilitate sediment transportation, resulting in constant fluctuations in regional connectivity patterns [37,45]. For instance, slope–channel connectivity transitions relate to the frequency with which channel processes rework materials derived from hillslopes, and channel–floodplain connectivity is driven by frequency and magnitude of flooding events [37]. Dynamically occurring landscape features affect sediment transportation to and through channels, effectively adding and removing transportation links. For instance, gully systems, which facilitate sediment transportation towards larger channels, often demonstrate disconnecting and reconnecting behaviour [46]. Conversely, buffers or barriers can impede sediment flow with different frequencies [37].

DPE processes may also be observed at a cosmological scale. Smolin [47] proposed that the pattern of star formations in spiral galaxies can be modelled as a propagation process along a network of dense gas clouds. For stars to form, a cloud of molecular gas must cool to a temperature that permits gravitational collapse. Cold cloud formations tend to be stable, but external perturbations can initiate a collapse [47]. A primary source of such perturbations is other recently formed stars and supernovae [48]. Consequently, star formation may be self-propagating [49,50]. Smolin [47] suggests that the pattern of observed star formations in many spiral galaxies can be explained if the connectivity of the propagation network repeatedly fluctuates across the critical density. Temperature oscillations required for these fluctuations may arise by feedbacks between two processes [51,52]: as the temperature falls, giant molecular clouds condense. External shocks then trigger the formation of new stars. Radiation from these stars heats the surrounding molecular gases, inhibiting further star formation. When the fuel of the heating stars is exhausted, radiation declines and the surrounding gases cool again to a level permitting star formation. Given enough molecular clouds, such a self-propagating network of star formation can maintain itself throughout large parts of a galaxy [47]. Notably, although not naturally occurring, alternating phases are commonly used in manufacturing. In industrial metallurgical processes involving manipulation of atomic lattices, repeated annealing is a standard technique for increasing material stability in products manufactured from many solid materials [53,54]. It works by rapidly heating and slowly cooling materials, thus breaking the connectivity of molecular bonding networks and letting them settle to a more stable configuration. The process must be repeated several times to achieve the stabilizing effect.

4.2. Ecosystems

Interactions among organisms form spatial networks that are structured by many processes, ranging from climatic to geological to ecological to socio-economic. For example, plants are confined to networks of habitat sites that are connected by dispersal. Processes that structure landscapes, such as fire, often induce phase changes in

Figure 2. The mechanism of DPE. Systems flip between poorly connected and well-connected phases. Perturbations or slow forcing—arising externally or internally—disrupt systems causing connectivity phase transitions in underlying networks. Internal pressures restore old and create new interactions.
Table 1. Summary of the role of DPE in some of the systems reviewed in §4.

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<tr>
<td>Network</td>
<td>Swamps connected by waterways</td>
<td>River channels connected by water flows across sandbars</td>
<td>Gas clouds connected by gravitational fields across space</td>
<td>Networks of molecules connected by molecular bonds in materials</td>
<td>Interacting species connected by migration on landscapes</td>
<td>Populations connected by migration on landscapes</td>
<td>Evolving species connected by ecological interactions</td>
<td>Activated neurons connected in a brain</td>
<td>Individuals connected in a social network, sharing information</td>
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<td>Phase Transitions</td>
<td>Floods and droughts isolate and reconnect local ponds</td>
<td>Droughts and floods isolate and reconnect river braids</td>
<td>Temperature oscillations: star formation heats clouds, which cool again when stars run out of fuel</td>
<td>Temperature oscillations: heating excites molecules; as they cool, they settle into more stable arrangements</td>
<td>Disasters remove populations across large areas, enabling interaction among previously isolated groups. Population growth fills this space</td>
<td>Habitat loss isolates subpopulations; adaptation and population growth reconnect them</td>
<td>Glacial cycles and larger scale mass extinctions fragment the ecological network; adaptation and speciation form new links</td>
<td>Relevant stimuli trigger increased activation of well-connected neurons; inhibitory feedback gradually inhibits this</td>
<td>Social conditions influence time spent in local versus global interactions, potentially shifting information transmission probabilities across the critical threshold</td>
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<td>Well-connected Phase</td>
<td>Coarse sediments are carried locally by flowing water; fine alluvium travels longer distances</td>
<td>Water flows faster along efficient braids, deepening channels, while overflows create new channels</td>
<td>Gravitational collapse in a cool cloud causes neighbouring clouds to collapse, initiating bursts of star formation</td>
<td>Molecules shift and reorganize themselves unpredictably</td>
<td>Individuals move and interact freely; competition removes less-adapted species and incompatible species combinations</td>
<td>Recombination eliminates unsuccessful and incompatible genetic combinations</td>
<td>Species grow and spread; ecological competition eliminates those stuck on lower local optima, and halts innovation</td>
<td>Widespread activation and chaotic firing, allowing information to spread through the brain</td>
<td>Numerous parties, Internet forums, conferences, publications and prominent media organizations</td>
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<td>Poorly connected phase</td>
<td>Coarse sediments solidify at the edges of water channels, forming protective levees. Fine soils sink to form soft, muddy swamps</td>
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<td>Warm clouds inhibit gravitational collapse, preventing propagation of star formation</td>
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<td>Molecules are strongly bonded to immediate neighbours</td>
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<td>Local species composition develops towards forms successful at a specific location</td>
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<td>Drift and local selection cause populations to diverge and adapt to new niches</td>
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<td>Adaptive radiation and speciation occur in populations suddenly isolated; new ecological conditions caused by loss of interactions spur innovation</td>
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<td>Local feedbacks allow subconscious processing of minor stimuli</td>
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<td>Interactions mainly within families, immediate colleagues and intimate friendships</td>
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<th>Outcome of DPE</th>
<th>Structures in landscapes: soft, deep swamps isolated by natural levees of firmer material</th>
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<td>Evolution of diverse and increasingly efficient river flows</td>
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<td>Ongoing creation of new star formations</td>
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<td>Increasingly stable solid materials</td>
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<td>Diverse ecological communities that are increasingly compatible and resilient</td>
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<td>Evolution of increasingly efficient modular gene networks</td>
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<td>Punctuated equilibrium; increasingly diverse, complex and flexible life forms</td>
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<td>Interaction of consciousness with lower level brain processes</td>
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<td>Potentially many effects on socio-economics, cultural diversity and change, and intercultural conflict</td>
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| References | [40–42] [39,41–44] [47,49,50] [53,54] [59–63] [56,119,132] [65,68,81] [85,86] [106,107,110] |
habitat connectivity for particular species [55]. Such phase changes may have profound ecological and evolutionary consequences, which we discuss below.

Ecological and evolutionary dynamics differ strongly between fragmented and connected habitat networks. Highly connected habitat networks allow processes such as population explosions, adaptive genes, diseases and predators to spread throughout a landscape, homogenizing selection pressures and potentially inhibiting local adaptation or even triggering extinction. Conversely, fragmented habitat networks may increase species extinctions through the gradual loss of isolated demes, increase genetic drift, reduce genetic diversity and reduce adaptive response to selective pressure [56]. For species that are adapted to disturbed or marginal habitat (e.g. weeds), fragmentation of undisturbed habitat often provides a connected network of disturbed habitat, hastening their spread [57,58].

The ecological impact of repeated cycles of phase transitions in habitat connectivity is illustrated by post-glacial pollen records of North American forests [59]. Species composition in forests remained largely static ('pollen zones') despite gradual climate change during this time, but underwent dramatic transitions following major fires [60]. Migrating species were constrained spatially owing to the overwhelming abundance of seed sources from dominant species, even though a changing climate might have favoured better-adapted invaders: it was only when dominant species were cleared away by fire that invading species could succeed. Fire-mediated zone boundaries have since been found at sites in many regions [61–63].

4.3. Living systems at evolutionary scales

For long-term evolutionary dynamics, the effects of repeated phase transitions in habitat networks are less transparent but no less crucial. Glacial cycles present a well-studied example. Cooling climates can result in falling sea levels, which create land bridges among islands, forming a connected habitat for many coastal species. Simultaneously, many widespread continental species have undergone repeated, drastic reductions in range during glacial periods. Owing to topography and other geographical factors, their habitats fragmented and these species became confined to a small number of isolated refugia [64]. While isolated in refugia, these species diverged genetically such that their modern-day descendents, although now well-connected throughout their geographical range, still exhibit marked patterns of population differentiation reflecting these periods of isolation [65].

Parallel patterns of post-glacial migration by multiple species out of the same refugia can explain genetic suture zones, which are geographical regions where numerous hybrid zones in different species co-occur along the same geographical lines [66,67]. These lines often also correspond to habitat barriers and range boundaries for adjacent-living sister species, suggesting that repeated glacial cycles act as an engine of speciation [65]. For example, meta-analysis of mitochondrial DNA studies in 63 bird species suggested that their adaptive radiations resulted from repeated population fragmentation events triggered by glacial cycles over the last 3 Myr [68]. Similarly, the evolution of new grasshoppers, macaques, pond-skaters, cicadas, bees, butterflies and beetles on Sulawesi has been attributed to habitat fragmentation caused by climate change [69].

Increasing habitat connectivity allows species to spread and diversify, implying that phase changes in habitat connectivity may rapidly transform biota across very large areas. Rapid evolution of new ecotypes and species is often traceable to the invasion of new habitats, especially when selection pressures are spatially distinct and mating is local [70,71]. For example, the shore-dwelling snail Littorina saxatilis underwent repeated parallel ecotype evolution within islands that arose in the last 10 000 years [72]. Similarly, replicate adaptive radiations in African cichlids followed their invasion of unoccupied lakes [73]; distinct stickleback ecotypes have arisen repeatedly following migration into streams [74]; and the apple maggot fly, an invader that arrived in the USA during the 1800s, has since diverged into several specialized forms that mate and feed on different native plants [75]. In each case, increased habitat connectivity allowed invasion of novel environments, triggering diversification.

Large-scale habitat fragmentation thus influences evolutionary novelty and diversity in several ways. Long-term isolated habitat patches are vulnerable to extinction [76], but facilitate genetic divergence through drift, local selection and sexual selection [77]. Newly connected habitats allow invasions by species, which may then diversify through ecological speciation (but also drive the existing species to extinction) [78]. Habitats that are connected over long periods permit the global spread of adaptations and well-adapted species, but eliminate less-competitive forms. Thus each connectivity phase, and the transition between the phases, provides fundamentally different evolutionary conditions.

A phase transition may also occur in evolutionary state-transition networks. Eldredge & Gould [79] documented the pattern of punctuated equilibrium: at large time scales, the fossil record is dominated by long periods of apparent stasis punctuated by mass extinctions, which are followed by brief periods of rapid change and diversification. Remarkably, the resultant qualitative pattern resembles that of the pollen record data described above, but on much larger time scales [80]. Gould [81] argued that evolving species rapidly reach local optima owing to the constraints of existing adaptations. Consequently, evolution of novel adaptations is confined to periods of reduced competition occurring mainly after mass extinction. In other words, the state-transition network for evolving species becomes sparser and ultimately fragments in the absence of disturbance; by deleting competitors, mass extinction provides a richly connected state-transition network for the survivors.

4.4. Perception and cognition

A number of seminal studies suggest that mechanisms involving connectivity phase changes may play an
important role in human perception and cognitive development.

One of the most influential theories in twentieth century psychology was Piaget’s theory of cognitive development [82,83], which is built around schemas: mental constructs used in perception, memory and problem-solving. Schemas are formed by two processes: assimilation and accommodation. Assimilation is the incorporation of new experiences into existing schemas, thereby refining and reinforcing them. Accommodation is the process of coping with novel situations by creating, combining and forming new schemas. Piaget proposed a development mechanism (equilibration) that mediates between phases of assimilation and accommodation. In a network model, where nodes represent schemas and edges their relationships, assimilation involves mainly local interactions, allowing new concepts to develop in relative isolation. In contrast, accommodation is a ‘global’ phase in which links can form between any relevant schemas.

Experiments by Freeman [84] showed that cognition involves sudden transitions in cortical electroencephalography oscillations. Sensory stimuli trigger rapid, chaotic firing of neurons. Subsequently, feedback loops gradually re-synchronize neural firing via a process of pattern selection. These changes suggest two apparent phases: the sensory stimulus flips the neural network into a phase of high connectivity and chaotic activity, followed by gradual decline in the overall activation and increasingly constrained local activity. Freeman conjectured that the sensitivity to initial conditions displayed by the cortex during these phase changes enhances the brain’s ability to discriminate sensory inputs [85,86].

Sergent & Dehaene [87] postulated that consciousness acts as a ‘global workspace’ for brain activity. In their model, sensory stimuli are normally processed subconsciously within local neural circuits. However, specific stimuli may become amplified by the local network, activating long-range connections, particularly via the fronto-parietal cortex which connects many different brain regions. This long-range activation can trigger a sudden, global activation at the whole-brain scale typical of conscious processing.

Extending the above ideas, the daily sleep–wake cycle suggests the possibility of other alternating phase transitions in the brain. In particular, dreams appear to play a crucial role. The nature of dreams is still far from clear, but among the many theories a common theme is to treat memory implicitly as a network. The nodes of this network have been variously interpreted as mental schemas (e.g. [88]), semantic memories (e.g. [89]) or other instances of perceptions and experiences. Arguably, waking hours can thus be regarded as a growth phase in which new nodes and edges are added to the network, and dreaming as a sorting phase, in which nodes and edges are reinforced or removed (e.g. [90]). Several authors have likened dreams to maintenance operations carried out when an information system is off-line (e.g. [91]).

4.5. Socio-economic systems

Methods and ideas based in network theory [92] and statistical physics are increasingly prevalent in the social sciences [93,94]. There is suggestive evidence that repeated phase transitions may occur widely in social networks and contribute to cultural evolution.

Local and global interaction patterns have been identified in various empirical studies. Cobb [95], for instance, analyses the role of local (personal) and global (corporate) networks in creation of reputation among competing offshore financial centres. Iori et al. [96] analyse the network topology of Italian overnight bank transactions and find recurrent increases in transaction density close to common month-end closing dates implying increased systemic risk owing to higher dependence and exposure. On a wider scale, Mann [97] analyses threats posed to nation states by modern socio-economical and geopolitical developments. He classifies political and socio-economic interactions into distinct networks according to their ‘distance’: local, national, international, trans-national and global. For instance, capitalist globalization increases the significance of international and trans-national networks, as a result of weakening the northern states (e.g. the EU), yet strengthening southern nation states by facilitating their economic development.

Some researchers see drastic social phenomena as phase transitions [98,99] and empirical studies show that social systems can exhibit basins of attraction. For example, Crane [100] shows that ghetto-like conditions spread through neighbourhoods in a way suggesting a critical threshold between constrained and global propagation dynamics. It has been suggested [101] that political revolutions are motivated by ‘preference falsification’—a critical transition in mass attitude resulting from a mismatch between individuals’ preferences drawn from personal versus public interactions. This situation can occur when people support a regime (e.g. for fear of prosecution) despite privately hating it.

Social networks lend themselves particularly well to the approaching social phase transitions with graph-analytical techniques owing to their explicit network structure. Since the seminal study [33] that led to the discovery of scale-free topologies (see also §§2.4 and 5.2), scientific co-authorship networks have attracted much interest. Numerous snapshot (e.g. [102]) and longitudinal studies (e.g. [103]) have been undertaken, including efforts to relate collaboration connectivity to geographical distance [104]. Connectivity transitions are observed in some, but not all social networks. For instance, as co-authorship links do not disappear, connectivity of such networks tends to increase monotonically.

Links in other types of social networks, however, can decay over time, and such networks tend to exhibit recurrent connectivity changes. A study of an email communication network in a university [105] showed significant seasonal changes in connectivity density leading to variations in size of the giant component. A longitudinal study of the Enron corporation email corpus [106] concluded that the communication networks become significantly denser and less hierarchical at times of crisis.

Detecting dynamic effects such as phase transitions in empirical data is inherently more difficult than detecting static properties such as scale-free or small world structures. It requires accurate empirical data
over extended time periods, which are becoming available for certain networks only now. Explanatory variables are typically numerous and cannot be manipulated, experiments are frequently unfeasible and are replaced by surveys and data often collected for other purposes [98]. As a result, simulation models of social networks have received wide attention.

Ehrhardt et al. [107] and Marsili et al. [108] showed that many social networks can exhibit sharp phase transitions. Ehrhardt et al. [107] demonstrated that in volatile environments social networks could exhibit emergent recurrent phase transitions in connectivity density, which are caused through internal feedbacks and without any external forcing or disturbances. Solomon et al. [109] studied a market percolation model of products through social influence and concluded that under simplifying assumptions, the connectivity density converges towards the critical threshold, and population sizes affected by products follow a power-law distribution. In many markets the distribution of such product impacts is bimodal [109]. It can be expected that under relaxed assumptions, the connectivity of the social influence network will fluctuate across the critical density leading to such distribution.

Castellano et al. [110] studied a model previously introduced by Axtell et al. [111], which investigates social consensus and demonstrates emergent dual-phase dynamics. In the model, agents exist on a lattice and communicate with their neighbours. Communication links are only active if agents agree and differ on at least one of their ‘cultural beliefs’ each, and agents become more similar in their beliefs during communication. Depending on parameter values, the model either converges on a dominant belief set or on a highly fragmented belief landscape with no active communication links remaining. In cases where a single belief set dominates, the active link density displays emergent connectivity phase transitions: initially it declines until it reaches a very low value, then it rises well over the percolation threshold and subsequently declines again until it reaches zero. In the real world, social groups do not exist in isolation. When groups that reached consensus come into contact, new active communications links appear. Thus, repeated cycles of creating active links and then using them to achieve new consensus can be expected to occur in real societies.

Economists increasingly realize that explicit characterization of different connectivity regimes is useful for understanding emergent phenomena [112], which cannot always be understood with the established analytical methods and traditional theories such as the general equilibrium theory or game theory [113,114]. These theories concentrate on specific kinds of interactions: in competitive general equilibrium theory, individuals interact with the market—global interactions; in game theory, individuals interact with each other—local interactions [115]. Many authors (e.g. [113,115]) stress that consolidating theories of economic interactions on different scales is central to understanding economy as a CAS.

Because cultural information is transmitted through social networks, cultural evolution may be influenced by phase transitions in these networks, similar to how biological evolution is influenced by phase transitions in landscape connectivity.

4.6. Models of modularity

Many natural systems, ranging from genomes to social networks to body plans and ecosystems, exhibit modular structure. However, the origins of modularity in these systems remain unclear. Recent models suggest that DPE may provide a mechanism for the evolution of modularity.

Changing environmental conditions affect the fitness landscape of evolving entities and thus the structure of the state transition networks (§2.2). Moreover, as evolution can be seen as a search problem for better adapted individuals, changing environments can affect the connectivity structure of the corresponding search space (see also §4.7).

Arguments from theoretical biology imply that repeated environmental changes that affect selection pressures acting on different traits may be the mechanism behind genetic modularity [28]: most individual traits are subject to stabilizing selection. However, depending on current environmental conditions, specific groups of traits can be subject to directional selection. Such trait groups are likely to evolve pleiotropic genes (genes that influence multiple traits). Conversely, genes that simultaneously influence traits that are subject to directional and stabilizing selection are likely to be selected against. Thus, genes involved in traits that are often selected for at the same time, may organize themselves into modules that are relatively independent from other trait modules.

The difficulty in formal mathematical and experimental treatment of biological CAS has promoted simulation models as a popular tool for their analysis. Several simulation models support the argument that recurrent environmental changes that induce connectivity transitions underlie the evolution of modularity. For instance, Kashtan & Alon [116] investigated the effect of changing environments on network evolution. They evolved digital circuits and neural networks with objective functions that repeatedly switched between different goals thus recurrently altering the connectivity structure of the search space. Each goal was composed of a different combination of sub-goals. The evolved networks contained densely connected functional modules that were loosely connected to the rest of the network. Network evolution in varying environments also led to the formation of network motifs [117] found in real systems, such as signal transduction and synaptic neuronal networks [116]. Subsequent work [118] showed that variability in environmental constraints increased the speed of evolution (decreased the number of generations required to match an objective function). Further experiments [119] showed that phase changes in habitat connectivity caused by induced extinctions lead to less specialization and increased modularity in internal structure of simulated organisms.

Similar results have also been obtained in numerical simulations. For instance, Lipson et al. [120] represented individuals as matrices. With increasing rate
of change of the target requirements, evolving matrices became less coupled and more modular. Variano et al. [25] investigated network properties of linear systems evolved using a genetic algorithm. They evolved directed graphs, each represented as an edge weight matrix $M$, and selected for linear stability of the resulting dynamical system, $x' = Mx$. The resultant networks were more modular and hierarchical than random networks with similar structural properties, and were robust to random rewiring. These simulations make few assumptions about the individuals or their environment, implying that modularity in network structures may be fundamentally associated with recurrent phase transitions in search spaces caused by varying environments [25].

### 4.7. Heuristic algorithms

Phase transitions within interaction networks are implicit in many optimization algorithms. They take the form of mediation between local and global search. For instance, in simulated annealing [121,122], the temperature schedule is used to arbitrate between local and global search steps. This corresponds to mediating between neighbourhood interactions (short search steps) and global interactions (distant search steps) between candidate solutions. Another example is the great deluge algorithm [123] that uses the analogy of a walker who walks around the solution space avoiding water floods of different levels. The water level thus controls the connectivity of the transportation network in the solution space acting similar to an annealing schedule and thus mediating between local (high water levels, poorly connected transportation network) and global (low water levels, well-connected transportation network) search. Similar ideas have been employed to improve the performance of a variety of optimization techniques that are prone to being caught in undesirable local optima when applied to non-smooth search spaces. This includes, for instance, the backpropagation learning algorithm for artificial neural networks (e.g. [124]), the particle swarm optimization algorithm (e.g. [125,126]), genetic programming (e.g. [127]) and support vector machines (e.g. [128,129]). In all these cases, the connectivity of the search space is changed from well-connected (global search, exploration) to poorly connected or disconnected (local search, exploitation). The phase transition occurs in that direction and only once or a few times. However, natural processes are typified by repeated connectivity phase transitions in both directions.

Arguably, optimization algorithms supplemented with simulated annealing style techniques may be improved by incorporating repeated connectivity phase transitions in both directions. For instance, this has been demonstrated by Kirley et al. in a modified version of the cellular genetic algorithm [130,131] based on insights from population dynamics and landscape ecology [132,133]. A population of individuals (candidate solutions) evolves on a grid with local competition and mating. The grid is subjected to intermittent ‘disasters’ that wipe out areas of the grid and making them temporarily unhabitable. This cellular genetic algorithm modified in this way outperforms the standard algorithm on a number of hard test problems [132,133]. Two interaction networks are important here. The network of populated grid cells determines the amount of gene (information) flow. When it is fragmented, the population evolves not as a whole, but as divergent sub-populations, which can slow premature convergence. The second is the network of the free grid cells. When this network is well connected, free cells can be repopulated without substantial fitness competition. Despite an initial fitness disadvantage, such candidate solutions can potentially evolve towards a different, possibly better local optimum. Similar ideas have been employed in a number of different parallel genetic algorithms; a comprehensive review is provided by Cantú-Paz [134].

Another way to gain advantage of the repeated changes in connectivity of the search space is based on combining genetic algorithms with Lamarckian evolution or the Baldwin effect. Lamarckian theory [135] held that traits acquired (learned) during a lifetime can be inherited into the next generation; the Baldwin effect [136] emphasizes the importance of selection for learning ability rather than for specific genetically ‘hardcoded’ abilities. In biology, Lamarckism has been displaced by Darwin’s evolutionary theory and the Baldwin effect remains debated, but both ideas have been applied successfully in computing (e.g. [137]). Artificial Lamarckian evolution uses local search at every generation to improve candidate solutions, which are then recombined through genetic operations that permit more distant jumps in the search space [138]. Conversely, when the Baldwin effect is applied to artificial evolution, results of local search performed at every generation are used to evaluate the fitness of candidate solutions, but are not fed back into the evolving genotypes. In non-smooth search spaces, the resulting selective pressure towards good starting points for local optimization helps direct the global evolutionary search [139]. For some optimization problems, hybrid methods between Lamarckism and the Baldwin effect have proven successful (e.g. [140]).

The Markov clustering algorithm (MCL) [141–144] is a further example for a heuristic algorithm based on repeated phase changes. The MCL finds cluster structure in graphs by simulating random walks without the need for additional information such as number of clusters or distances between cluster items. The algorithm is based on two alternating operations. The first operation (‘expansion’) computes a power of the Markov matrix that defines the graph. This computes the probability of multi-step transitions along the graph and reinforces intra-cluster links. The second operation (‘inflation’) computes a power $> 1$ of each matrix element. This reinforces stronger links in relation to weak links. This process of repeated flips between intra-cluster interactions and direct neighbour interactions eventually leads to the separation of the graph into different clusters. The MCL has proven successful in identifying cluster structure in networks obtained from empirical data (e.g. [145]) and from simulation studies (e.g. [146]).

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5. APPLICATIONS

In this section, we survey studies that apply the DPE framework to provide insights about specific important issues in complexity theory.

5.1. Network structures

Recent research [12,14] has revealed a number of mechanisms that can lead to important network topologies, including scale-free [32] and small-world [34]. The emergence of other topological properties, such as hierarchy and modularity, is less well understood (compare §2.4). DPE processes can facilitate the formation of many network structures. For instance, the formation of small-world structures via DPE is straightforward: they can be built from a regular network with only local connection patterns; global phases need only add long-range connections, thus creating short-cuts in paths between nodes. Below, we examine how DPE may lead to scale-free and modular networks.

5.2. Scale-free structures

Scale-free networks (§2.4) are found in a variety of complex systems, such as scientific collaboration networks [33], protein-interaction networks [147], telecommunication networks including the Web [148] and many others [149]. Scale-free topology is thought to facilitate the emergence of widespread complex properties such as epidemic spreads [150], random fault tolerance and random disturbance resilience [151], and the small-world property [34].

Traditional generative models for scale-free networks are based on preferential attachment in growing networks [32], a process where new nodes are added to the network and connected to the existing nodes with a probability proportional to their degree. However, scale-free structures occur in many natural networks of fixed size, such as functional adult brain networks [152]. Some generative models for scale-free networks of fixed size have been proposed (e.g. [153,154]); however, these models are highly synthetic and unlikely to correspond to any natural process.

Paperin et al. [155] demonstrated that DPE may generate scale-free structure in networks of fixed size. A network structure was generated based on a dual-phase interaction schedule with different types of interactions in local and global phases. In the local phase, nodes selected randomly with probability proportional to their degree interacted with neighbours that were selected randomly with probability inversely proportional to their degree. In the global phase, low degree nodes interacted preferentially with high degree nodes anywhere in the network. Local interactions destroyed structural edges and global interactions resulted in new edges. Simulations showed that over time the node degree distribution approached a power law [155]. Analysis of similar generative models may explain the appearance of scale-free properties in natural networks of (approximately) constant sizes. For example, preferential attachment is often used by individuals as a heuristic for optimizing social networks [156]. In a growing group, this mechanism can generate scale-free topology [32]; however, most societies have approximately constant size [157]. Owing to selection pressure, individuals attempt to forge connections to popular individuals and to break connections with less popular group members. This corresponds to the above abstract model: well-connected entities tend to break edges to poorly connected neighbours while poorly connected entities seek to create edges to well-connected ones.

5.3. Modularity and hierarchical organization

Although generative models for modular networks are known, the conditions that produce them in CAS remain obscure [158,159]. As discussed in §§3 and 5.4, DPE can flip a network between selection-dominated balance phases (high connectivity) and variation-dominated exploration phases (low connectivity). Sub-systems that remain internally stable during a variation phase can form new interactions to other sub-systems and assume new roles in a changing system. In this way, they become functional components during subsequent variation phases, leading to the emergence of modular structures. When emerging functional components already exhibit modular structure, the above mechanism can lead to hierarchical organization.

The above conjecture is supported by a recent study [155] of a network model. The model nodes are connected by weighted edges, and have a similarity measure defined on a single discrete-valued attribute. When two nodes interact, they either establish a new edge or increase the corresponding edge weight. The weights of unused edges decay over time. The node interactions occur according to the two DPE phases. In the local phase, the nodes interact with their first- and second-degree neighbours and with other similar nodes. In the shorter global phase, all nodes interact randomly. This DPE process leads to the formation of richly connected modules in an otherwise less well-connected network. These modules tend to persist over time with very few changes, whereas the topology connecting the modules to each other tends to vary more strongly over time leading to complex modular structures (figure 3).

The need for both local and global connections is apparent: predominantly global interactions lead to a single, densely connected super-module, whereas predominantly local interactions lead to fragmentation into separate sub-structures with no cross-connections. Further work [160] showed that the temporal separation of phases enhanced functional organization in simulated genomes, demonstrating that networks with simultaneous global and local connections (such as small worlds) do not lead to the same outcomes as DPE.

In DPE systems, nonlinear feedbacks within networks can amplify or suppress stimuli. Selection provides a kind of ‘system memory’ in these networks because the network structure at any time is the product of its evolutionary history. Adaptively relevant information from past events remains encoded in the current network, even if current selection pressures are different. This memory effect is not captured in systems modelled using equilibrium statistical mechanics, and
may distinguish CAS from simpler systems in their responses to DPE.

5.4. Sustained diversity and perpetual novelty

There is much evidence that CAS generally self-organize towards stable, diverse states, but our understanding of how typical CAS properties emerge remains limited. We suggest that DPE provides a widespread natural mechanism for sustained diversity and perpetual novelty in CAS.

Analytical [161,162] and computational [163] models show that lower order local dynamics (e.g. feedback processes) can stabilize systems over a large range of external forcing, and that higher order local dynamics (e.g. evolutionary processes) can greatly increase the stabilizing effect. Established ecosystems, for instance, are somewhat resilient against forcing that could drive them away from current attractors [21,80,164]. However, the adaptive forces that underlie global stability of CAS also inhibit novelty. Stabilizing selection acting on system components at various scales, as well as on topology and interactions, may drive a system as a whole to a local optimum state, halting innovation [165]. Coevolution, wherein system components adapt to one another, may result in feedback loops which provide some ongoing novelty. However, coevolution seems unlikely to account for the innovation observed in many CAS. For instance, current models suggest that selection, not variation, drives speciation and that coevolutionary feedback loops probably rapidly (on evolutionary time scales) lead to stable local optimum states [19].

We suggest that perturbations can cause systems to flip from high-connectivity phases dominated by stabilizing selection to low-connectivity phases of evolutionary exploration leading to ever new and diverse adaptations. As discussed in §§4.2 and 4.3, evolutionary innovations often coincide with external perturbations. External disturbances may affect both system components and interaction networks, thus moving systems away from local optima (and so increasing the connectivity of corresponding state-transition networks). While a disturbed system remains far from a fitness optimum, any chance variation of local components or substructures may provide a better adaptation to the local constraints and selection will facilitate the proliferation of such change. Over time, components and their interactions at multiple scales are driven towards new local optima and selection again inhibits variation and stabilizes the system (state-transition network connectivity decreases). Future perturbations continuously affect the system and flip it between different connectivity phases leading to ever new and diverse adaptations.

The above process has been exemplified in a simulation model of adaptive radiation in landscapes [35]: in the model, organisms normally exist within a connected landscape where selection maintains a stable composition. Intermittent disturbances disrupt landscape connectivity, fragment populations and free-up areas of empty space. Results show that in the presence of disturbances, species diversity and the number of used habitat niches are significantly higher than in scenarios without disturbances. This is explained by the different selection regime and evolutionary variation during repopulation of disturbed areas.

6. DISCUSSION: RELATIONSHIP WITH OTHER THEORIES

DPE is related to several other key concepts in CAS research. Here we briefly review two widely used concepts—SOC and AC. By emphasizing network-theoretical approaches and empirical observations from a variety of adaptive and non-evolutionary complex systems, we show how DPE complements both ideas.

6.1. Self-organized criticality

SOC [166,167] implies that CAS self-organize to a critical state, in which the complexity of systems’ responses to external stimuli emerges through a propagation of the stimuli through an interaction network with thresholds at each component. The thresholds effectively control the propagation connectivity near the critical threshold between the connectivity phases, resulting in propagation avalanches of different sizes. In this sense, SOC suggests that CAS evolve to reside
in a transitional state at the boundary between stasis and chaos.

Langton coined the term ‘edge-of-chaos’ to describe the above transitional state [17,18] in the context of studying cellular automata (for a comprehensive review of cellular automata, see [168]). He found that cellular automata of a certain class, termed Wolfram class 4 [169], exhibited dynamics similar to systems that are thought to be dominated by SOC processes. Langton [18] conjectured that computationally universal and various other ‘interesting’ cellular automata are located within that class. This conjecture was supported by some studies (e.g. [170]), but later evidence [171] has shown that the arguments were not conclusive.

The size of propagation avalanches in SOC systems follows a power-law distribution. The presence of this distribution in data is often taken to indicate that a system may self-organize to a critical state. A number of models [166] led to suggestions that various complex systems, including many CAS, exhibit SOC dynamics. For instance, it has been suggested [172] that as the sizes of extinction events observed in the fossil record follow a power-law distribution, punctuated equilibria [79] may be a result of the biosphere’s self-organization to a critical state. However, the extent to which SOC presents a general form for the organization of CAS remains unclear. Many SOC models concern complex systems that are not subject to selection and in many cases there are several processes which may lead to power-law-distributed data. For instance, Newman [173] demonstrates a non-critical extinction model without any species interactions. That model yields a power law with an exponent that is closer [163] to the empirical-punctuated equilibria data than the SOC model [172]. Several authors (e.g. [174,175]) suggest that the critical behaviour requires fine-tuning of an order parameter. Furthermore, it remains unclear whether SOC occurs in non-conservative systems [174,176]. The notion of ‘nearly critical behaviour’ avoids some of the problems related to SOC and can be applied to a wider range of systems (e.g. [176]). Recently, Eliazar & Klafter [177] have shown analytically that 1-on-f noises, traditionally thought to indicate SOC dynamics, can generally emerge from a superimposition of many independent stochastic signals. In summary, the presence of power-law data may not always imply self-organization towards critical dynamics.

DPE mechanisms may be involved in non-critical systems that produce power-law data. In §5 we discussed that many CAS tend to self-stabilize, while external stimuli perturb them away from their attractors and increase the connectivity of state-transition networks. To describe this using SOC vocabulary: under SOC, systems self-organize towards a critical region; under DPE, systems rather develop towards a settled state, and disturbances repeatedly push systems across the critical region, towards a chaotic state (in the sense that responses to random stimuli and variations are unpredictable), from which systems return to a new settled state, accumulating order and complexity on the way (figure 4).

Notably, the DPE and the SOC paradigms are complementary, not contradictory. The magnitude of DPE oscillations (i.e. how far system dynamics deviate from critical during different phases) may vary significantly according to specific circumstances. Thus, recognizing whether a particular phenomenon is caused by a truly critical attractor or by a repeatedly unsettled non-critical attractor may be difficult.

A further consequence of a network topological approach to systems analysis is that power-law data can also be produced by non-critical systems with underlying scale-free networks. For instance, the distribution of sizes of random fault-affected subnets in some telecom networks follows a power law owing to the scale-free nature of the networks and not owing to any critical interactions [178].

6.2. The adaptive cycle

Another influential concept in CAS theory is the AC [80]. The AC extends the idea of ecological succession [179], and is predominantly applied to ecological and socio-ecological systems, especially with reference to ecosystem management.

The AC is closely related to the concept of ‘panarchies’ [80,180]—a metaphor that describes the hierarchical relationships in dynamical systems of different scales. The AC is a metaphoric concept [164] suggesting that the behaviour of many socio-ecological systems exhibits cycles consisting of four qualitative phases.

— A growth and exploitation phase (designated $r$), in which new or freed-up areas and niches are rapidly populated by opportunistic organisms.

— A conservation phase ($K$) signified by competition, selection and resource accumulation.

— A collapse or release phase ($\Omega$), in which accumulated resources are catastrophically released, often mediated by disturbances.

— A reorganization phase ($\alpha$) in which the remains of an $\Omega$-collapse are reorganized and restructured.

The bulk of the literature on ACs [181] is concerned with empirical studies (e.g. [182,183]), secondary data analysis (e.g. [184,185]) and applications to human-managed systems (e.g. [186–188]). However, some work has been undertaken to provide a causal explanation for the AC (see [80] for an overview). Most of this work concentrates on ecosystem resilience and threshold dynamics [21,80,180]. Empirical studies attribute typical CAS properties to each phase of the AC. For instance, resilience against external forcing is expected to be high during the $r$ and $\alpha$ phases but low during $K$. Resource availability is high during $\alpha$ and $K$ phases, but low during $r$ and $\Omega$. Connectedness of control variables is maximal near the end of a $K$-phase.

The AC and DPE concepts are complementary. The DPE framework aims to incorporate a wider range of CAS from different subject domains and has important parallels to the AC.

— The balance (high connectivity) phase in DPE loosely corresponds to the $r$–$K$ transition in AC. This phase is signified by stabilizing selection,
increasing connectivity and growing potential for propagation of disturbances.

— The variation (low connectivity) phase in DPE loosely corresponds to the $O-\alpha-\tau$ transition in AC. This is a phase of innovation and reorganization of underlying networks.

Notably, connectedness in AC refers to the richness of interactions of control variables $[80,180]$. In fact, however, there may be several interaction networks with different connectivity regimes within a system at any one time. For instance, species in food webs and populations in landscapes form interaction networks that act simultaneously on the same groups but may have very different topologies. The network of control variables interactions may thus have very different properties from the interaction network of specific system components.

In summary, the DPE framework encapsulates many ideas from SOC and AC. It adds to their explanatory power, for instance by providing network-theoretically grounded explanation for power laws in some non-critical systems and by extending the applicability of the balance-variation cycle concept beyond socio-ecological systems.

7. CONCLUSIONS

In this review we set out to highlight the role played by networks in natural and artificial systems. Networks are inherent in all complex systems, and patterns and processes that occur within the underlying networks play a major role in the emergence of system-wide features ($\S 2$). Perhaps the most widely felt network processes are changes in edge density, especially the connectivity avalanche ($\S 2.3$). As our review showed ($\S 4$), phase changes occur in complex systems of many kinds. What is more, in almost every case, those phase changes can be traced to connectivity avalanches within underlying networks.

Recurrent phase changes in network connectivity play a key role in emergence and self-organization within many kinds of systems ($\S 4$). Our review reveals several mechanisms that can produce these connectivity phase transitions, including external disturbances, slow forcing resulting in the crossing of attractor basin boundaries and internal feedbacks. Moreover, the two connectivity phases often display the features that characterize DPE. That is, a low-connectivity phase where isolated components evolve independently, and a high-connectivity phase where these components may interact and recombine, so that the system as a whole evolves in synchrony. As a result, systems can become more complex, modular, creative and better-adapted, when subject to DPE.

Some of the effects of DPE, such as its contribution to perpetual novelty ($\S 5.4$) and optimization in systems under selection ($\S 4.7$), are well established in models and can be clearly linked to empirical phenomena such as geomorphic evolution ($\S 4.1$), ecological responses to climate change ($\S 4.2$) and adaptive radiation after mass extinction ($\S 4.3$). In other cases, such as socio-economic ($\S 4.5$) and neural network development ($\S 4.4$), the effects of DPE have yet to be clearly demonstrated, despite the existence of plausible mechanisms.

Relating perception and cognition to its neural network substrate is a key challenge in current psychological research. Brains exhibit behaviours suggesting the spontaneous emergence of dual phases ($\S 4.4$). If the DPE processes suggested here can be generalized, repeated phase changes in neural network activity may play a crucial role in cognition through selective processes at the neural level, which could contribute to self-organization of brain modules. Modeling the behaviour of neural networks under DPE would provide a strong test of the generality of the DPE framework.

Similarly, the self-organization of societies and cultures is now seen as crucially responsive to network structure ($\S 4.5$). Cultural behaviour evolves on social networks through a form of selection, and these networks have been shown to undergo recurrent connectivity phase changes. It remains unknown, however, whether these systems exhibit the modular and adaptive properties that occur in ecological and genetic systems under DPE. Further modelling and empirical research is required to test this possibility.

Interpreting processes such as DPE has already revealed several new useful insights (e.g. [35,155,189,190]).
It has also suggested new methodologies, such as the modified cellular genetic algorithm (§4.7), and generative models for network topologies (§5.2).

There may be other DPE phenomena yet to be discovered. Complexity theory helps to recognize deep similarities between completely different fields, and it is impossible to identify, let alone discuss, all pertinent phenomena in a single work. We look forward to future research that will fill these gaps. Conversely, not all complex systems exhibit DPE, nor is it the only mechanism by which interesting network and evolutionary structures can arise. For example, DPE does not appear as a driving force in the evolution of scientific collaboration networks or the growth of the Internet.

This problem raises the crucial issue of validation. Firstly, DPE itself calls for further investigation. Should DPE be seen as a single underlying process or as a family of related processes? An important practical problem is how to identify DPE processes from empirical observations. In particular, how can they be distinguished from other phenomena that drive the emergence of complexity? Currently, intensive simulations based on detailed empirical data are required to test the relevance of DPE in any particular scenario.

Another important matter is the role of distinct phases dominated by local or global interactions. What phenomena depend on such phases with a well-defined transition, and what can also be caused by stochastic occurrences of local and global interactions, such as in small-world networks? Research shows that distinct phases can lead to superior adaptation and self-organization in simple genetic systems, compared with stochastically occurring local and global interactions [160]. However, it remains unclear when and if this result applies in natural systems.

DPE can induce modular and other interesting network topologies; however, the conditions under which it will do so are not well understood. Development of a mathematical theory for DPE could provide strong predictions about the conditions required, the possible effects and relevant natural systems. The increasing availability of detailed longitudinal datasets for many evolving networks further provides numerous opportunities to study the effects of phase changes in different empirical systems [13,191].

Different areas of research in emergent and complex systems share a number of key questions [11]. What are the mechanisms behind the emergence of modularity? Why are scale-free structures omnipresent, even in non-critical systems? How does perpetual novelty arise in adaptive systems? Research reviewed here shows that DPE is one mechanism involved into these complex phenomena.

Explicitly characterizing common mechanisms aids cross-fertilization between disciplines. Network theory and related methods from statistical physics have found applications in social sciences (§4.5), ecology and evolutionary biology (§§4.2 and 4.3). Other areas where DPE phenomena appear to occur, such as cognitive neuroscience (§4.4), may also benefit from those techniques.

As a science, complexity theory still suffers from its recent origins. Related phenomena are still interpreted using a wide variety of terminology, concepts and methods that are usually specific to particular fields of research: ‘Perhaps there can be a general theory of complex systems, but it is clear we do not have one yet’ [192]. Identifying common processes such as DPE is an essential step towards the goal of understanding complexity.

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