Multilevel Selection Shaping Adaptive Social Networks

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Abstract

Understanding how human and non-human animal social networks evolve through emergent properties and feedback mechanisms is essential for explaining their adaptability and persistence. Collective social niche construction refers to the process where individuals, through their interactions, actively shape the social environment, resulting in network structures that influence individual behaviours and drive the emergence of adaptive properties. These emergent properties arise from these interactions, producing complex and efficient networks capable of optimising communication, cooperation, and problem-solving. Processes as self-organisation and phase transitions demonstrate how localised interactions can trigger critical transitions, rapidly restructuring network topology to enhance adaptability under changing conditions. These self-organized processes are fundamental to the Cumulative Cultural Brain Hypothesis, which proposes that increasingly complex and efficient networks foster the development of advanced cognitive abilities and social learning. The resulting enhancement of communication and information processing, in turn, facilitates further network complexity and efficiency, creating a positive feedback loop that supports cultural accumulation and resilience. This perspective integrates insights from evolutionary biology, behavioural ecology, and network science to highlight the dynamic and adaptive nature of social networks, where self-organisation and cumulative processes continually reshape network topology to meet ecological and social demands.

Keywords: sociality, social behaviour, optimality, social evolution, self-organisation

Introduction

Since the beginning of humanity, we as humans have faced various pressures that affect our survival and the way we interact with each other (Boyd and Richerson 2004; Harari 2014; Henrich 2017). These pressures shape the development of social relationships and the construction of social networks (Dunbar 2024), thereby influencing our ability to gather, process, and disseminate information, which varies in scale and complexity from individual decision-making to collective knowledge. The recent COVID-19 pandemic has vividly underscored these dynamics, with social distancing becoming a crucial measure to limit pathogen spread. This phenomenon mirrors adaptive behaviours in the animal kingdom (Battesti et al. 2015; Borgeaud et al. 2017; Sosa et al. 2021a; Maeda et al. 2021), where species modify their social interactions – quantitatively (e.g. number and frequency of contacts) and qualitatively (e.g. nature and strength of interactions) (Moscovice et al. 2020) – to optimise fitness and mitigate risks, such as disease transmission (Romano et al. 2020).

These modifications can lead to the formation of isolated social clusters or closed groups, balancing the trade-off between infection risk and access to essential resources or information. This dynamic interaction creates a feedback loop between individual social decisions and the emergent properties of social networks, encompassing both individual-level adjustments and collective-level changes, such as network modularity or division of labour. This emphasises the crucial role of adaptive social structures in responding to environmental challenges. As Darwin noted, natural selection is not solely based on individual traits and genetic inheritance; it also encompasses a broader range of influences, including population dynamics and cultural transmission. Selection pressures act on various levels, going beyond the traditional scope of inclusive fitness theory (Nowak 2006; Nowak et al. 2011), and this multifaceted selection process drives the evolution of complex behaviours and social structures, demonstrating that genetic, epigenetic and cultural evolution are essential in shaping adaptive responses and social networks (Jablonka and Lamb 1998; Henrich and McElreath 2003; Claidière et al. 2014; Birch and Heyes 2021; Ashe et al. 2021). These processes are underpinned by a network of feedback mechanisms, where interactions between individual, cultural, and environmental factors recursively shape selection pressures and evolutionary outcomes.

In his work on alternative brains (Solé et al. 2016, 2019; Macia et al. 2017), Ricard Solé explores how different brain architectures can be seen as neural networks selected through evolutionary processes to gather, process, and disseminate information effectively. This concept of neural network selection parallels the selection of social network structures in animal societies (Pelé and Sueur 2013; Sueur 2023). Complex and seemingly adaptive networks are observed across various levels of biological organisation (Oltvai and Barabási 2002; Do and Gross 2022). By investigating the mechanisms and selective pressures that influence social relationships and network structures (Moscovice et al. 2020), we aim to elucidate how individual strategies and interactions contribute to the evolution of, much like neurons in a brain form complex, adaptive networks to enhance cognitive function (Bullmore and Sporns 2012; Clune et al. 2013). However, we also aim to discuss about the adaptive nature of connectivity, whether within a brain or a social group, underscoring the role of the network topology in enhancing the fitness and survival of individuals and groups.

Social Attraction and Social Avoidance Affecting Social Networks

Social attraction and social avoidance, which involve the aggregation or repulsion of individuals, are widespread behavioural strategies that individuals use to balance the costs and benefits of group living. Some socio-ecological pressures, such as predator defence and access to reliable information, lead to social attraction, while others, like resource competition and the risk of pathogen transmission, lead to social avoidance (Moscovice et al. 2020). Despite this, the biological literature has paid little direct attention to how individuals manage the fitness trade-offs between these two strategies. The increasing evidence of plasticity in social network structures (Stroeymeyt et al. 2018; Sueur et al. 2021; Testard et al. 2024) raises key questions about the interaction between social attraction and social avoidance and their influence on the emergent properties of social networks under varying conditions (Romano et al. 2021, 2024). Investigating how individuals respond to specific trade-offs can enhance our understanding of the mechanisms and selective pressures that shape social relationships. Modular networks (Newman 2006) emerge in conditions where interactions are costly, involving only a few individuals, whereas beneficial interactions are more evenly distributed among all individuals in the group or in cooperative subgroups (Marcoux and Lusseau 2013; Sah et al. 2017; Romano et al. 2018). These findings highlight the importance of examining opposing pressures to understand the complexity of individual relationships and the resulting

diversity in social structures across animal societies (Sueur et al. 2019; Romano et al. 2020, 2021).

Individual decisions influence their social environment, which subsequently impacts the selection pressures driving individual behaviour (Sueur et al. 2019; Cantor et al. 2021). The concept that sociality is shaped by selection pressures acting on individual social and non-social phenotypes is not novel. However, the dynamic relationship between individual behaviour, social structure, and information/pathogen transmission (or avoidance and attraction) has only recently been examined in detail (Romano et al. 2018, 2020, 2021; Evans et al. 2020; Ashby and Farine 2022). Co-evolution of strategy and network structure in sender-receiver games can lead to the formation of distinct groups and hybrid signalling behaviours, enhancing communication efficiency in social networks (Fulker et al. 2024). In essence, access to information or the risk of infection leads to changes in an individual's social behaviour, resulting in alterations in its centrality within a network. This subsequently influences the network's topology, creating a more or less subdivided (modular) network, which affects how information and pathogens are transmitted throughout the network. The mechanism by which an individual's behaviour impacts the social structure and environment, leading to fitness gains, is termed 'collective social niche construction' (Sueur et al. 2019; Sueur 2023). This idea extends the 'niche construction' perspective commonly found in behavioural ecology (Odling-Smee et al. 1996; Day et al. 2003; Laland and Brown 2006; Laland and O'brien 2011; Laland et al. 2016). The consequences of cultural and/or biological evolutionary forces acting on these individuals at the network level remain largely unknown. The study by Brush et al. (2018) demonstrates how conflicts of interest among individuals can enhance the collective computation of social structures. In many biological systems, the functional behaviour of a group is collectively computed by the system's individual components. An example is the brain's ability to make decisions via the activity of billions of neurons (Bogacz 2007; Marshall et al. 2009; Pelé and Sueur 2013; Solé et al. 2019). A long-standing puzzle is how the components' decisions combine to produce beneficial group-level outputs, despite conflicts of interest and imperfect information. Researchers (Bogacz 2007; Marshall et al. 2009; Bogacz et al. 2010) derive a theoretical model from mechanistic first principles, illustrating that conflicts of interest can improve the accuracy of group-level outcomes despite individual components having imperfect information. This model emphasises the role of information accumulation and aggregation phases in collective decision-making, showing that conflicts, when managed properly, can lead to more accurate and adaptive social decisions and structures. This aligns with the broader concept of how individual behavioural strategies influence social network dynamics and stability, particularly under varying ecological and social pressures. Modeling is essential because it allows us to explore emergent processes that are difficult to intuitively grasp from observing individual interactions alone.

Genetic and Cultural Selection as Driving Forces of Network Topology Changes

Various examples illustrate the connection between socio-ecological pressures and social network topology. Natural selection impacts individual traits, including behavioural ones, which then influence social network structure, affecting individual survival and reproduction. Behavioural traits play a crucial role in altering social network properties in response to ecological pressures. Animals can be aggressive or tolerant, more or less nepotistic, which will affect the network topology (see for instance the Parasite Stress Theory, Fincher and Thornhill 2012; Thornhill and Fincher 2014). Natural selection operates through genetic and

cultural selection. Intergenerational transmission of behaviour occurs either genetically or via social learning, with variation and selection shaping biological and cultural evolution.

Behavioural traits can be targeted by genetic selection, influencing social network structures. Genotypic variance affects personality traits, which are heritable and define inter-individual behaviour variations (Dingemanse et al. 2010; Réale et al. 2010). Personality, comprising boldness, activity, sociality, exploration, and aggressiveness, influences network connections. For instance, aggressive individuals often attract fewer group members, leading to less dense but more modular networks (Sueur et al. 2011; Puga-Gonzalez et al. 2018). Conversely, bold individuals may become central in their groups, increasing network centralisation (Aplin et al. 2013). Group composition of individual personalities alters social network structure in experimental populations of forked fungus beetles (Cook et al. 2022). Genetic variance in individual interaction patterns impacts group network topologies, suggesting that indirect genetic effect models are necessary to understand social network evolution (Bijma and Wade 2008; Bijma 2011). Specific genes, such as serotonergic and oxytocynergic profiles, influence social behaviours like aggression and kin preference (Williams et al. 1994; Lesch et al. 1996; Brent et al. 2013; De Wilde et al. 2017). How individual changes their social relationships with age, known as social capital, as observed in humans, macaques or ants (Almeling et al. 2016; Lucas and Keller 2020; Rosati et al. 2020; Sueur et al. 2021), might be seen as an adaptation at different levels.

Culture, defined as group-specific behaviour transmitted through social learning, represents a secondary evolution form (Dawkins 2006; Whiten et al. 2017; Sueur and Huffman 2024). Social information and learned behaviour allow faster and better adaptation to environments than genetic learning. Social networks influence cultural evolution, as seen in dolphins and humpback whales, where behaviour spread follows network topology (Donaldson et al. 2012; Mann et al. 2012; Cantor et al. 2015). Cultural evolution also affects social networks through positive assortment and homophily, where individuals prefer interacting with others showing similar behaviours (Morgan and Laland 2012). This mutual influence process, including conformity, leads to network changes (Henrich and Boyd 1998; Cialdini and Goldstein 2004). Game theory and social networking studies show that individuals with similar strategies prefer to interact, increasing fitness and modifying network topology (Ohtsuki et al. 2006; Skyrms and Pemantle 2009). Prestige and learning from key individuals also influence cultural evolution and social networks, enhancing network efficiency for information exchange and potentially affecting fitness (Henrich and Gil-White 2001; Migliano et al. 2017). Integrative anthropology emphasises the interconnectedness of biological and cultural factors in human evolution, advocating for a comprehensive approach that includes contemporary evolutionary theory and human cultural complexity (Fuentes 2016) that needs to be extended to other animal societies (Sueur 2023).

Feedback Loop Between Individuals and Networks

An under-explored question is whether networks of individuals can outperform individuals acting in isolation. In a recent experiment, researchers tested how humans modify their social interactions and, consequently, network topology in response to changing environmental conditions (Almaatouq et al. 2020). They found that network plasticity and environmental feedback (based on participants' performance) could improve individual judgments, allowing groups to outperform individuals working in isolation. Under full feedback conditions (where all participants' performance is public information), dynamic networks became more centralised. Networks with higher adaptation rates (i.e. high sensitivity to changes in agents'

performance) performed better in changing environments, whereas less adaptive networks implied longer periods of social learning, reducing errors in more stable environments. These findings highlight network plasticity as a key adaptive mechanism refining individual actions. Regarding social transmission trade-offs, the adaptiveness of a network influences how individuals are affected by information and pathogen pressures (Romano et al. 2020, 2021). But what makes a network 'adaptive'?

Behavioural traits in individuals can be selected over generations through genetic variance (genetic evolution) or social learning (cultural evolution), directly influencing the topology of social networks. For causal factors like predation and food distribution, and intermediary mechanisms such as mating systems, the social network topology results from combined individual strategies that affect fitness (Sueur et al. 2019; Moscovice et al. 2020; Dunbar 2024). However, the pressure-individual-network triad may function differently for infectious agent risk and information sharing as one individual cannot directly make strategies for changing its number of partners or contacts changing the whole flow of transmission. Simply put, an individual located on one side of a social network cannot influence the relationships of conspecifics on the other side of the network with whom it has no direct contact. In such cases, the network topology itself may hold intrinsic value, providing benefits to all group members regardless of their individual social strategies.

For example, high network modularity, resulting from the sum of individual choices facing ecological pressures, can decrease pathogen transmission (Griffin and Nunn 2012). Similarly, network efficiency plays a significant role (Sueur et al. 2013; Pasquaretta et al. 2014). This can be compared to the selfish herd theory, where individuals at the centre of a spatial group are less predated than those at the periphery, but peripheral individuals also benefit from the dilution effect (Hamilton 1971; Foster and Treherne 1981; Delm 1990). However, individual decisions are not isolated; the actions of one individual can influence the social environment and indirectly affect the relationships, behaviour, and fitness of other conspecifics. For instance, a highly connected individual may facilitate the spread of information or pathogens, impacting the health and knowledge of others in the network. Conversely, a socially avoidant individual may disrupt information flow or alter group cohesion, indirectly affecting the adaptive potential of the entire network. Such individual effects can propagate through social networks, reshaping interactions and influencing overall network topology. In social networks, this translates to network topology representing a trade-off between individual strategies to achieve a certain centrality based on first-order metrics (degree and strength or weighted degree for food access, reproduction, or protection from predation) and the social transmission of information and disease which is more dependent on second order metrics as clustering and betweenness (Firth et al. 2017; Sosa et al. 2021b). Thus, the selection of certain network properties in some circumstances may enhance the fitness of not just some, but all group members.

Structure-dynamic interplays have been studied for years by network scientists. For example, Gross and Blasius (2007) introduced the concept of the dynamics on and of networks, demonstrating that local dynamics determine the state of nodes, leading to temporal changes in network topology ('topological evolution'). These topological changes, in turn, influence local dynamics, completing the feedback loop. Networks exhibiting such feedback loops are termed 'adaptive' or 'coevolutionary' networks by Gross and Blasius (2007).

From Individual to Multilevel Selection

In animal societies, ‘adaptive’ can be interpreted as responsive since biological adaptation implies natural selection. Researchers suggest that a multilevel selection process may occur if individuals with behavioural traits favouring a specific network topology – which increases fitness of the group members – are selected through biological or cultural evolution (Gross and Blasius 2007; Fisher and McAdam 2017; Sueur et al. 2019; Cantor et al. 2021). This is not indicative of group selection but rather the network-level outcome of a given behavioural phenotype. This discussion extends to group phenotypic composition (Farine et al. 2015). Group phenotypic composition refers to the combination of individual phenotypes within a group and how their interactions and variations shape group-level dynamics and emergent properties, which in turn influence individual fitness and evolutionary outcomes. This concept supports adaptive network hypothesis by demonstrating how emergent properties from individual decisions and interactions contribute to network structure and adaptability.

To observe network evolution, selection should be considered at multiple levels rather than solely at the group level (Traulsen and Nowak 2006; Fisher and McAdam 2017). Social networks in mammals or birds, where most group members are kin, and eusocial insect colonies, where members are not genetically identical, can be likened in terms of selection dynamics. While individuals are the basis of selection, the network’s structure is crucial for the survival and fitness of group members (Gross and Blasius 2007; Do and Gross 2022), similar to the importance of hive structure in eusocial insects (Bonabeau et al. 1997; Camazine et al. 2003). It is not a problem to think that complex behaviour as collective one are shaped by selection (Walsh et al. 2020, 2022), so why not about social network topology?

Extending consideration to populations over multiple generations is essential. Behavioural ecology often examines how behaviours relate to fitness and mediate relationships between traits (e.g. morphology and physiology) and fitness. However, this approach can limit the application of evolutionary principles to social networks, despite some studies examining global network outcomes (Ohtsuki et al. 2006; Fisher et al. 2016; Allen et al. 2017; Puga-Gonzalez et al. 2018). A holistic view of networks, considering how individual choices impact behaviour and fitness, can offer insights into sociality evolution. In similar environments with identical ecological pressures, populations displaying behavioural traits that enhance group network modularity (through genetic or cultural evolution) may show higher survival rates during disease outbreaks. Individual exchanges between populations could lead to one behavioural phenotype, coding for a specific network topology, replacing another or to the stable existence of several phenotypes. As for the group phenotypic composition, the network topology might be selected through a combination of individual behavioural strategies, social interactions, and multi-level selection pressures that drive in return phenotypic covariance among interacting individuals as seen in the stickleback (Neumann and Bell 2023), ultimately impacting fitness and evolutionary dynamics (Farine et al. 2015). Thus, social network traits might be determined by multilevel selection, favouring specific behavioural phenotypes at both individual and global levels (Fisher and McAdam 2017). Indeed, both individual and group behaviour (strategy as a collective decision or network topology) can influence individual fitness, but multilevel selection is rarely quantified on social behaviours. Costello et al. (2023) used a contextual analysis to measure the effects of individual network position and group network structure on fitness in forked fungus beetles. It was found that high individual connectivity and centrality increased male mating success, while group network structure did not, and that females had lower reproductive success in populations with many social interactions, highlighting the differential impacts of social behaviour on fitness between males and females and the influence of habitat structure on multilevel selection.

Network topology significantly impacts individual fitness but is not solely dependent on individual social strategies. Multilevel selection typically favours phenotypic variation (Farine et al. 2015; Costello et al. 2023), producing mutualistic benefits for all group members (Nonacs and Kapheim 2007). Evolutionary processes may favor the 'coding' of group phenotypic composition for a network topology, termed 'collective social niche construction'. (Sueur et al. 2019). This network topology should remain stable under consistent ecological conditions but be resilient or adaptable when conditions change.

Collective social niche construction

Niche construction is a concept in evolutionary biology that refers to the process by which organisms alter their own and each other's environments, often modifying the selection pressures they face (Odling-Smee et al. 1996; Day et al. 2003; Laland and Brown 2006; Laland and O'brien 2011; Laland et al. 2016). This modification of the environment can have significant implications for evolutionary processes. There are two main interpretations of niche construction: selective niche construction, which focuses on how organisms' modifications of their environments affect their fitness and that of their descendants, and developmental niche construction, which emphasises how these modifications contribute to development and inheritance (Kaiser et al. 2024). To refine this concept, niche construction can be understood as involving modifications that create a positive feedback loop, where environmental changes actively enhance adaptive advantages or developmental outcomes, rather than merely reflecting incidental impacts of organisms on their surroundings.

Selective niche construction (Kaiser et al. 2024) describes how the persistent modification of environments by organisms creates selective pressures that influence the fitness of those organisms and their offspring. This concept suggests that the activities of organisms, such as building nests or creating social structures, can shape the evolutionary trajectories of populations by creating environments that favor certain traits over others. Developmental niche construction, on the other hand, focuses on how organisms influence the development and inheritance of traits across generations. This involves the transmission of non-genetic resources, such as modified environments or social behaviours, that enable the generation and maintenance of heritable phenotypic variation. For example, parental care behaviours that shape the developmental environment of offspring can lead to stable transmission of certain traits and behaviours, influencing evolutionary outcomes.

Social niche construction refers to the process by which animals actively create and modify their social and physical environments to enhance their adaptive strategies and long-term interests (Yamagishi and Hashimoto 2016). This concept views behaviour as a strategy shaped by stable and predictable responses from others within specific social structures. These structures provide the incentives that guide individuals' behaviours, ultimately shaping and being shaped by the collective actions and adaptations of the group (MacKinnon and Fuentes 2011; Fuentes 2016). This concept was proved from fruitflies (Saltz and Foley 2011) to macaques (Flack et al. 2006).

The concept of collective social niche construction extends these ideas to social networks. Social networks in animal societies are formed and shaped by the interactions and behaviours of individuals. Just as niche construction alters environmental selection pressures, the structure and dynamics of social networks can influence the selection pressures acting on individuals within those networks. Social networks can enhance or constrain the flow of information, the spread of pathogens, and the distribution of resources with competition or

cooperation, thereby affecting individual fitness and social organisation (Marcoux and Lusseau 2013; Sah et al. 2017; Romano et al. 2018, 2024).

Collective social niche construction provides a framework for understanding how social structures evolve in response to ecological and social pressures. It highlights the importance of considering both genetic and cultural selection in shaping social networks. Cultural evolution, driven by social learning and information transmission, can rapidly alter social network structures, influencing the adaptive landscape of populations. Similarly, genetic selection on individual traits, such as personality and social behaviours, can lead to the emergence of distinct network topologies that enhance group fitness. However, the emergence of distinct network topologies is not exclusively driven by genetic factors. For instance, transitions between gregarious and territorial social structures can arise through ontogenetic development, where age-related changes in behaviour influence social strategies. Similarly, learning processes, such as individual experience and environmental feedback, can shape social interactions, leading to dynamic shifts in network organisation. Cultural influences, including the transmission of behaviours and traditions within a population, can also drive changes in network topology, creating flexible structures that adapt to new ecological or social contexts. These mechanisms demonstrate that the diversity of network structures observed in nature results from the interplay of multiple processes – genetic, ontogenetic, experiential, and cultural – all of which contribute to the evolution of sociality.

By integrating the concepts of niche construction and social network evolution, collective social niche construction offers a comprehensive perspective on the adaptive nature of connectivity in animal societies. This approach underscores the role of the network topology in enhancing the fitness and survival of individuals and populations, providing a valuable lens through which to study the evolution of sociality.

Cumulative cultural brain hypothesis and social networks

Humans are an undeniably remarkable species with massive brains, amazing technology, and large, well-connected social networks. The co-occurrence of these traits is no accident. The Cultural Brain Hypothesis and the Cumulative Cultural Brain Hypothesis provide a framework to understand the evolutionary processes that led to the expansion of brain size and complexity in humans and other taxa (Muthukrishna and Henrich 2016; Muthukrishna et al. 2018). According to these hypotheses, brains have been selected for their ability to store and manage information, acquired through asocial or social learning. This selection process creates a feedback loop between brain size, adaptive knowledge, group size, social learning, and the juvenile period. The Cultural Brain Hypothesis posits that larger brains facilitate greater social learning and innovation, while the Cumulative Cultural Brain Hypothesis suggests that this leads to a positive feedback loop, driving further increases in brain size and cultural complexity. These processes are deeply intertwined with human social structures, which are characterised by diverse, dynamic and efficient network topologies (Henrich 2017).

For example, central place foraging, a key feature of early hunter-gatherer societies, likely facilitated the development of complex social networks by changing patterns of mobility and increasing opportunities for information exchange (Garg et al. 2021). This process also entails the competitive selection of information, where individuals or groups prioritise certain types of knowledge over others, akin to the dynamics observed in honeybee hives. According to the Information Center Theory (Zahavi 1977), communal gathering points, such as roosts or hives, serve as hubs where information about resource availability is shared, contested, and

refined, enhancing collective decision-making efficiency. This adaptation of social ties (Almaatouq et al. 2020) is supported by evidence from behavioural and psychological studies, showing that humans intentionally form and adjust their social networks to enhance collective learning, memory, and problem-solving capabilities. Memory, in this context, operates at multiple levels: it can be stored within individuals, within units, or within the structure and patterns of the network itself, serving as a site of collective memory (Thomas and d'Ari 1990; Anastasio et al. 2012). By collective memory here, we meant that the network topology affects as feedbacks the individual behaviour as Hinde (1976) suggested. This concept aligns with the idea of hysteresis, where the history of a system influences its current state and allows for multiple stable solutions depending on past conditions. From the scale of genes to societies, hysteresis illustrates how networks retain and adapt information over time, thereby shaping their resilience and functional diversity (Couzin 2007). This process of memory consolidation across scales demonstrates how structural and behavioural patterns emerging from interactions within networks can act as repositories of information, enhancing adaptability and collective intelligence. For example, from the scale of genes to societies, hysteresis illustrates how networks retain and adapt information over time, shaping their resilience and functional diversity. The dynamic nature of these networks allows for adaptation to environmental and social changes, improving collective intelligence and decision-making. Such adaptive changes of social structures is crucial for fostering creativity and innovation (Baten et al. 2020), as individuals tend to follow high-performing peers, thereby enhancing their own creative outputs. Moreover, humans employ strategies like prestige-biased social learning (Brand et al. 2020), where they preferentially learn from highly respected and successful individuals, efficiently acquiring adaptive information. This highlights a contrast with traditional approaches to self-organisation, which often anonymize individual actors in favour of emphasising emergent network properties. By contrast, prestige-biased learning underscores the importance of specific, identifiable actors whose roles and influence can significantly shape the dynamics and outcomes of the network. This structuring of social networks not only supports cooperation but also maintains social hierarchies conducive to collective benefits (Lozano et al. 2020), illustrating the profound impact of human cognition and cultural inheritance on the topology and functionality of social networks.

Cumulative cultural brain hypotheses linking with adaptive networks in humans is well illustrated (Henrich 2017). However, is there something similar that can be found in other animals? Pasquaretta et al. (2014) found that the neocortex ratio is correlated with network efficiency in primates. Such network properties affecting individual fitness could be shaped by natural selection. These results align with the social brain and cultural intelligence hypotheses, which suggest that the importance of network efficiency and information flow through social learning is related to cognitive abilities. A recent finding (Testard et al. 2024) shows that macaques are able to adjust their social tolerance after a hurricane, facilitating access to scarce shade critical for thermoregulation. This illustrates a broader principle of behavioural modulation based on physiological states, where individuals adapt their social strategies to meet immediate survival needs, such as temperature regulation, resource access, or recovery from stress. Why not observe this adaptive response in the context of social network topologies, as seen with responses to epidemics in different animal species (Romano et al. 2020)? Indeed social networks predict brain structure in rhesus macaques (Testard et al. 2022) but also in baboons (Meguerditchian et al. 2021) reinforce the feedback loop between individual-level and network-level (Sueur et al. 2019).

Phase Transitions, Self-Organization and social networks

While the Cultural Brain Hypothesis and the Cumulative Cultural Brain Hypothesis emphasise the role of positive feedback loops in driving brain expansion and cultural complexity, it is essential to acknowledge that positive feedback mechanisms do not merely result in gradual accumulation. Instead, they often involve amplification effects that push systems beyond critical thresholds, resulting in phase transitions or emergent properties. This dynamic is not exclusive to brain evolution but is also evident in other domains, such as behavioural flexibility in social insects and cellular differentiation. For instance, in social insects, positive feedback mechanisms enhance collective intelligence, allowing colonies to transition from disorganised states to highly efficient organisational structures (Couzin 2007; Krause et al. 2010; McMillen and Levin 2024). Similarly, in cellular differentiation, feedback loops involving cross-inhibition and molecular signalling contribute to the formation of distinct cell types, as highlighted by Waddington's epigenetic landscape (Wang et al. 2011). These processes illustrate how positive feedback not only amplifies existing structures but also generates new organisational patterns and adaptive functionalities. Moreover, this concept extends to social network evolution, where behavioural interactions (e.g., affiliative or agonistic signals) can create self-organized patterns reminiscent of Turing models (Maini and Woolley 2019) that explain natural pattern formation, such as stripes and patches but may also explain network clusterisation (Li et al. 2023; Luo et al. 2024; Pranesh et al. 2024). Thus, understanding how positive feedback loops operate across various levels of biological organisation can provide valuable insights into the evolution of complex social structures and adaptive networks. In many species, self-organisation processes may conduct to adaptive networks in the same way that it conducts to efficient complex collectives (Bonabeau et al. 1997; Couzin and Krause 2003; Hemelrijk 2005; Gross and Blasius 2007; Puga-Gonzalez and Sueur 2017; Do and Gross 2022). Adaptive networks in various species often emerge through self-organisation, a process that underscores the intricate interplay between evolutionary pressures and inherent organisational principles. Simple rules, which dictate interactions and adjustments based on local information, lead to the self-organisation of adaptive networks (Do and Gross 2022). Through processes such as preferential attachment (Nowak 2006; Poncela et al. 2008; Fotouhi et al. 2019), where nodes link to highly connected nodes, or rewiring, where nodes alter their connections to optimise local conditions, complex global structures form. These emergent properties include dynamic critical states resembling phase transitions, spontaneous division of labour into distinct functional classes, and intricate topologies that enhance information flow and resilience. Thus, the interplay of basic local interactions drives the evolution of sophisticated adaptive networks that can efficiently respond to environmental and internal changes.

Phase transitions in networks describe abrupt changes in network topology resulting from variations in internal or external parameters, such as social interactions, environmental conditions, or biological processes (Vicsek 2007). These transitions are particularly relevant to the concept of collective social niche construction, where feedback loops between individual decisions and emergent network properties shape the evolution of social structures. In adaptive networks, the self-organised interplay between local interactions and global network dynamics creates conditions where minor changes in individual behaviour can lead to critical transitions, resulting in shifts from decentralised, modular structures to centralised or highly connected topologies (Schweitzer and Andres 2022; Romanczuk and Daniels 2022). Such transitions are analogous to the critical phenomena observed in other complex systems, where self-organized criticality and network optimisation processes drive structural changes that enhance resilience, information flow, and adaptive capacity (Gross and Blasius 2007). Furthermore, phase transitions provide a mechanistic explanation for how social systems can rapidly reorganise in response to environmental or social pressures, such as predation risk,

resource availability, or disease spread (Das et al. 2024). Notably, abrupt changes in network structures can also arise from variations in dominance styles, where more tolerant or despotic social systems produce different modularity and centrality patterns (Puga-Gonzalez and Sueur 2017; Puga-Gonzalez et al. 2018). Additionally, pressures related to disease and information transmission can shape the modularity of networks, as individuals selectively interact to balance benefits from information access and avoid costs from pathogen exposure (Romano et al. 2024). This dynamic process of adaptation and network restructuring demonstrates how phase transitions contribute to the evolution of social networks by enhancing collective decision-making, cultural transmission, and long-term resilience through emergent structures optimised for specific socio-ecological contexts.

Conclusion

Adaptive social networks are shaped by the dynamic interplay between individual behaviours, social structures, and environmental pressures. Collective social niche construction highlights how individuals actively influence their social environment, generating emergent network properties that optimise fitness and information flow. Mechanisms like social attraction, social avoidance, self-organisation, and phase transitions drive network formation, evolution, and resilience. The Cumulative Cultural Brain Hypothesis suggests that increasingly complex networks enhance cognitive abilities and cultural accumulation, creating feedback loops that reshape network structures.

By integrating insights from theoretical morphology, network science, and multiscale biological architectures, we can better understand these adaptive networks. The concept of a 'network morphospace' (Avena-Koenigsberger et al. 2015) where networks are mapped based on shared connectivity traits, helps identify the generative rules and constraints shaping network evolution. Network geometry (Boguñá et al. 2021), encompassing shortest paths, latent spaces, and dynamic processes, reveals fundamental symmetries like fractality and scale invariance, crucial for applications from brain function to the network topology. Additionally, biological systems exhibit a multiscale architecture, with each level – from molecules to animal groups – solving distinct problems through collective dynamics (Couzin 2007; Centola 2022; McMillen and Levin 2024). This nested and functional structure highlights how collective intelligence drives adaptive functionality across scales.

Glossary

Adaptive networks: Networks that dynamically adjust to environmental and social changes to improve resilience and information flow efficiency.

Behavioural traits: Characteristics of individual behaviour, such as aggression, sociability, or tolerance, often influenced by genetic and environmental factors.

Cultural evolution: The process by which behaviours, traditions, and knowledge are transmitted and modified within a population through social learning, often faster than genetic evolution.

Emergent properties: Features or behaviours of a complex system (like a social network) that arise from interactions among its components but cannot be predicted from the properties of individual elements.

Feedback loop: A process where the outputs of a system influence its inputs, either reinforcing or regulating the system (e.g. individual decisions influence network structure, which in turn affects individual behaviour).

Genetic selection: The process by which certain genetic traits increase in frequency within a population due to their survival or reproductive advantages.

Modularity (network modularity): A measure of network structure that describes the division of a network into subgroups that are densely connected internally but sparsely connected with others.

Niche construction: The process by which organisms actively modify their environment or that of other species, thereby influencing the selection pressures they face.

Social attraction and avoidance: Behavioural strategies involving the approach or avoidance of others to maximise benefits (e.g. predator defence) and minimise costs (e.g. resource competition).

Social learning: The acquisition of behaviours through observing or imitating others, often a key driver of cultural evolution.

Topology (network topology): The arrangement and structure of connections within a network, influencing how information or resources flow.

Plasticity (network plasticity): The ability of a network to adapt or reconfigure in response to environmental or social changes.

Self-organisation: The spontaneous emergence of complex structures or behaviours in a system based on simple rules, without centralised control.

Cultural Brain Hypothesis: The idea that the evolution of larger and more complex brains is linked to the development of social and cultural capabilities.

Homophily: The tendency of individuals to interact primarily with those who are similar to them in behaviours, attitudes, or other characteristics.

Division of labour: The distribution of tasks among members of a group or system, often seen in complex social networks to enhance efficiency.

Pathogen spread: The transmission of diseases or pathogens through social interactions or networks.

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