Social Complex Systems as Multiscale Phenomena: From the Genome to Animal Societies

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Abstract: For decades, researchers have studied animal social phenomena and aimed to answer: What is social complexity? Are some animals more socially complex than others? However, social complexity concepts are far from agreed and the field is still open to new research approaches. In this position paper, we propose to frame social complexity as a problem of organized complexity (whereby multiple scales and interactions across components produce patterns and organization). To improve our understanding of sociality, we encourage building a "social complexity theory" at the intersection of complex systems, behavioral ecology, and social systems concepts. This manuscript highlights the importance of considering social complexity as a multiscale phenomenon and raise the presence of trade-offs between scales. We illustrate the relationship between complexity and scales with examples from genomic to population scale in animal societies. Moreover, we suggest giving special attention to genome-scale studies to provide a common ground for comparing complexity among animal species and put forward comparative genomics as an approximation to drive the understanding of the evolution of social complexity.

1 INTRODUCTION

In 1947, Warren Weaver proposed to divide scientific problems into three levels of complexity depending on how variables are treated. The first level named "the two-variable problems of simplicity" deals with pairwise relationships and is exemplified by the physical science before 1900. The second level is represented by "problems of disorganized complexity", wherein methods can deal with billions of variables using probability theory and statistical mechanics (e.g., the motion of the stars which form the universe, or the fundamental laws of heredity) (Weaver, 1948). These approaches are two extremes in a complexity range that leaves the impression that scientific inquiry has concentrated its efforts in an extremely incomplete two-variable description of the world or, in the opposite extreme focusing on dealing with an astronomical number of variables. Despite the number of variables, the outcome seeks the same: to provide a simplified view of the world that overlooks the diversity of complex phenomena.

According to Weaver (1948), the middle area of the range has been devoid of attention. The main feature of this middle region does not regard the number of variables but on its interactions and their tendency to produce patterns and organization. Here lives Weaver's third level of complexity problems, called "problems of organized complexity", which deal simultaneously with a sizeable number of variables interconnected into an organic whole.

Waver suggests that these problems cannot be handled with statistical techniques aimed at simplicity; instead, science must embrace these problems of organized complexity differently if intended to answer questions such as: Is a virus a living organism? How do genes organize to express all the features of an individual? Do molecules "know how" to replicate their pattern?

In this position paper, we elaborate on some ideas important to the study of animal sociality from the perspective of complex systems. Here we propose that social complexity is a problem of organized complexity and raise social complexity as a multiscale phenomenon. In our view, this approach may get us closer to address questions such as: What is social complexity? Can social complexity be measured? Are some animals more socially complex than others? And if this is the case, why?

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2 A SUMMARY OF THE STUDY OF SOCIAL COMPLEXITY

For decades, researchers have tried to establish links between evolution, ecology, sociality, and cognition to explain why some species evolved to form complex societies. However, social complexity is still poorly understood (Hobson et al., 2019). The complexity of social systems seems to vary across species. Animal societies vary in size, composition, number of social units, reproductive skew, parental care, cooperation, and competition. This diversity is the outcome of multiple social solutions that could have originated from different evolutionary paths to fit in a wide range of niches. (Hobson et al., 2019; Kappeler, 2019; Kappeler et al., 2019).

According to Freeberg et al. (2012), complex social systems can be defined as “those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time”. This definition emphasizes interactions among agents as the core aspect underlying socially complex instances. Therefore, it is a fertile conceptual substrate to explore alternative definitions based on complex system concepts.

Different authors have provided multiple definitions of social complexity, some examples are: 1) More complex societies are those with many individuals; 2) More complex societies are those where groups have social roles, such as members of morphologically different castes; 3) Complex societies are those with multiple levels of social groups; 4) Complex societies are those where social relationships between group members can be individually differentiated (Bergman and Beehner, 2015; McShea and Brandon, 2010; Freeberg et al., 2012; Kappeler et al., 2019; Rubenstein and Abbot, 2017).

In line with multiple definitions, multiple approaches have been used to estimate social complexity, mostly based on taxonomic dependent traits, making comparative studies hard to implement or even unviable. Some recent attempts have been made to unify concepts and make social complexity studies more accurate. Kappeler et al. (2019) proposed a framework for the systematic study of social complexity based on four components: social organization, social structure, mating system, and care system. Despite this framework provides a comprehensive set of recognizable features useful to characterize and compare social species, it does not deepen on how to conceptualize and quantify complexity in this context (Hobson et al., 2019).

A different proposal was made by Holland and Bloch (2020), who argues that “we need to switch the measure of complexity in individual social traits from semantic discussions to quantitative social traits that can be correlated with molecular, developmental, and physiological processes within and across lineages of social animals”. To achieve this goal, they suggest combining key social complex traits into multidimensional lineage-specific quantitative indices, thus enabling comparisons across species. However, Hobson et al. (2019) point out that, although multidimensional approaches may improve comparisons of social systems, combining these measures is unlikely to provide additional information on social complexity.

Empirical studies on social complexity are becoming common. Therefore, it is important to notice that an appropriate conceptualization of social complexity is critical before “jumping into quantifying it”. The main behavioral characteristics of any complex system are emergence, adaptability, and dynamism. But currently, social complexity studies based on single traits fail to account for system-wide organizing properties and limit the understanding of the social system as a whole, resulting in a mischaracterization of large-scale behavior (Aziza et al., 2016; Hobson et al., 2019; Siegenfeld & Bar-Yam, 2020).

Besides theoretical problems, according to Kappeler (2019), questions concerning distribution and determinants of social complexity represent important open questions for future research. Therefore, efforts to improve understanding of social complexity are needed; and comparative studies can advance understanding of which traits and mechanisms influence, or are influenced by, the evolution of social complexity (Holland and Bloch, 2020).

Hobson et al. (2019) affirm that one way to evaluate and compare the level of complexity of animal societies is to incorporate some of the fundamental concepts of complex systems theory(Hobson et al., 2019)(Hobson et al., 2019). These authors highlight three concepts that apply to animal social systems: (1) Scales of organization: scales, levels, and perspectives that constitute complex systems, from which they can be described; (2) Compression: an information-reduction process that summarizes or abstracts patterns in observations and (3) Emergence: local interactions between components give rise macro-level order phenomena, like those documented in animal movement and problem-solving studies. These concepts are not intended to be direct measures of social complexity, but rather should be used as a guide when using or developing approaches to social complexity.

A practical way to study social complexity is with computational simulations, defined as “the imitation overtime of the operation of a real-world system or process”. Systemic approach simulations consider the system as a whole and focus on the dynamic relationships between its components, allowing to do virtual experiments to test different scenarios and make predictions of the behavior of a system (Aziza et al., 2016)

When talking about social complexity, it is important to keep in mind that the description of a system depends on the level of detail used to describe it. To fully characterize a system it is necessary to understand it across multiple scales (Siegenfeld and Bar-Yam, 2020). Therefore, we consider it is important to recognize social complexity as a multiscale phenomenon and that this notion is useful to reconcile the diversity of definitions that abound in the literature.

3 SOCIAL COMPLEXITY AS A MULTISCALE PHENOMENA

“As far as I am able to judge, the conditions of life appear to act in two ways --directly on the whole organization or on certain parts alone and indirectly by affecting the reproductive system. With respect to the direct action, there are two factors: namely, the nature of the organism and the nature of the conditions… The former seems to be much the more important; for nearly similar variations sometimes arise under, as far as we can judge, dissimilar conditions; and, on the other hand, dissimilar variations arise under conditions which appear to be nearly uniform. There can, however, be little doubt about many slight changes, such as size from the amount of food, colour from the nature of the food, thickness of the skin and hair from climate, etc.” (Darwin, 1859).

In this quote from The Origin of the Species, Darwin mentions two factors that can directly affect organisms, the nature of the organism and the nature of the conditions -Also referred to as Nurture and Nature respectively, terms coined by Richard Mulcaster in 1581, and later used on the long opposition debate about the relative importance of heredity and environment on behaviors- (Pinker and Pinker, 2014). The nature-nurture controversy is still ongoing. Biologists have accepted that genes, the environment, and interactions between them affect behavioral phenotypes; however, it “retains the flavor of the nature-nurture dichotomy”, which influences research in this field (Robinson, 2004). Thus far, nature and nurture have been raised as two different phenomena, each one explaining a relative part of social behaviors. But what if they were both expressions of the same phenomena at different scales?

Social behaviors are complex phenotypes exhibited by individuals that belong to complex systems, and complex systems deploy through many spatio-temporal scales. Sociality is composed of micro-level actions that aggregate to produce meso- and macro-level phenomena. Depending on how individuals interact with each other at the micro-social level, different types of social states can be produced at the macro-level (Hobson et al., 2019).

To illustrate the importance of scales when studying complex systems, consider the following example: if we compare a human and a gas containing the same number of molecules that are in the human body, but with no particular arrangement, which system is more complex? (Siegenfeld and Bar-Yam, 2020).

On a microscopic scale, it is more difficult to describe the positions and velocities of all the molecules of the gas than it is to do the same for all the molecules of the human (thus, the gas seems more complex). At the human scale, a gas looks quite simply, because behaviors will only be perceived when involving trillions of molecules, and there are few behaviors of gases involving so many molecules (thus, complexity seems lower). On the other hand, human behaviors get more complex as the level of detail increase, “the description will first include the overall position and velocity of the human and then the positions and velocities of each limb, followed by the movement of hands, fingers, facial expressions, as well as words that the human may be saying” (Siegenfeld and Bar-Yam, 2020).

If we use the same approach to describe a society, from macro to micro scale, its description starts on societies, moving to individuals, individuals are built from organs and these are composed by tissues, which in turn are constituted by individual cells. At scales smaller than that of a cell, complexity further increases as one sees organelles, followed by large molecules such as proteins and DNA, and then eventually smaller molecules and individual atoms. This incredible multiscale structure is a defining characteristic of complex systems (Siegenfeld and Bar-Yam, 2020)

Social scales can be useful to compare sociality across species, to describe different levels of their organization, to highlight the features of sociality (Hobson et al., 2019), and to better contextualize studies based on specific social traits.

The advances in genome sequencing and comparative genomics provide the opportunity to move forward the nature-nurture debate. Nowadays it is clear that DNA is both inherited and environmentally responsive, and that behaviors are “orchestrated by an interplay between inherited and environmental influences acting on the same substrate, the genome” (Robinson, 2004).

4 SMALLER SCALE: ARCHITECTURE AND COMPLEXITY OF THE GENOME

“For complexity at larger scales, there must be behaviors involving the coordination of many smaller-scale components“ (Siegenfeld and Bar-Yam, 2020). According to this statement, to produce socially complex behaviors, the genome components must be somehow organized to ensure this coordination under ever-changing environmental conditions.

A genome provides all the information the organism requires to function (Nature education, 2014). The genome has a non-random architecture (Lynch, 2007b; Wolf, 2003). Koonin (2009) defined ‘genome architecture’ as the totality of non-random arrangements of functional elements in the genome (e.g., genes, regulatory regions). This architecture is not fixed; it is shaped by evolutionary forces like recombination, mutation rate, and transposable elements that give place to differences in the genome architecture (e.g. ploidy levels, gene copy number variation, chromosomal inversions, and novel genes) (Gokcumen et al., 2013; Koonin, 2009; Rubenstein et al., 2019; Yeaman, 2013). The variations in the genome architecture can be evidenced within the tree of life; from small and packed genomes with overlapping genes in viruses (Firth and Brown, 2006), to compact genomes organized in operons with intergenic regions and few gene overlap in prokaryotes (Lillo and Krakauer, 2007; Rogozin et al., 2002), to genomes with protein-coding sequences organized in intron-exon structure in eukaryotes (Lynch, 2007a; Lynch, 2007b).

But how does genome architecture influence the complexity of the genome? The zero-force law of evolution states that any evolutionary system with variation and heredity will tend to diversify and increase in complexity because these are both variance quantities that spontaneously increase as errors accumulate in time (McShea and Brandon, 2010). Michael Lynch’s theory (Lynch, 2007a; Lynch 2007b; Lynch and Conery, 2003) states that genetic changes that increase the complexity of genome architecture are slightly deleterious and fixed only when purifying selection is weak. In large populations, purifying selection is strong, so the “complexification threshold” cannot be surpassed, producing compact genomes. On the contrary, genomes of small populations (e.g. eukaryotes) are beyond the threshold, so the complexification of the genome is possible (Koonin, 2009).

But under which circumstances is complexity beneficial? According to the Law of Requisite Variety, an effective system must be at least as complex as the environment to which it must react. If a system must be able to provide a different response to each of the 100 environmental possibilities it is presented with, then that system should at least explore 100 possible actions (Valentinov, 2014). Under this scenario, how is this “complexity threshold” regulated? Following complex systems notions, macro-level dynamics emerging from micro-level interactions can ‘feedback’ to constrain micro-level interactions and dynamics within the range of variability that ensures persistence (Hobson et al., 2019). This negative feedback stabilizes not only micro and macro-level behaviors but also imprints tradeoffs between traits at different scales of the organization.

5 HIGHER SCALE: RELATIONSHIP BETWEEN THE COMPLEXITY OF THE GENOME AND SOCIAL COMPLEXITY

As social complex behaviors are influenced by numerous genes (McShea and Brandon, 2010), it is reasonable to ask how did independent genes evolve to ensure the level of coordination needed to sustain sociality? One hypothesis is that genes are clustered together within a region of a chromosome and inherited as a single unit, potentially regulated in concert, as supergenes, such as the case of the non-recombining portions of the sex chromosomes (Campagna, 2016; Rubenstein et al., 2019). These supergenes play a key role in the evolution of complex adaptive variation (Brelsford et al., 2020). For example, the White-throated bird coloration and mating behavior are determined by a supergene (Campagna, 2016), and also is the polymorphic social organization of Formica ants (Brelsford et al., 2020). These cluster genes phenomena also admit an explanation based on complexity theory, which explains that complexity at large scales requires the coordination of many smaller-scale components. Due to this coordination, complexity at a small scale is limited, because the coordination depends on interdependencies between the interacting parts (Siegenfeld and Bar-Yam, 2020)

Sociogenomic studies also support the idea that behavioral phenotypes are underpinned by clustered and organized genes, as the so-called "toolkit" genes, a set of deeply conserved genes that consistently regulate the development of similar morphological phenotypes across many species(C. C. Rittschof & Robinson, 2016; Clare C. Rittschof et al., 2014; Shell & Rehan, 2019). Toolkit genes related to odorant receptors ordered in tandem have been found in several social species such as honeybees and ants, possibly linked to chemical communication(Kent et al., 2019). Gene expression studies of vertebrates suggest the existence of behavioral gene sets for male polymorphisms (*for* FoxP2 and its orthologs), possibly related to speech, song, and other types of vocalizations. Other studies have found gene clusters in multiple complex phenotypes, some examples are: homeobox genes, enzymes of the same metabolic pathway, olfactory receptors, vertebrate immune system, and plant-pathogen response(Bear et al., 2016; Ebstein et al., 2010; Koonin, 2009). Overall, evidence suggests the convergent evolution of genetic toolkits, calling attention to its underappreciated role in the evolution of complex traits(Bear et al., 2016; Donaldson & Young, 2008; Liu et al., 2016; C. C. Rittschof & Robinson, 2016; Clare C. Rittschof et al., 2014).

6 COMPLEXITY ON DIFFERENT SCALES: TRADE-OFF BETWEEN GENOME COMPLEXITY AND SOCIAL COMPLEXITY

According to “the agency theory” all living organisms pursue a goal (Walsh, 2015), and to achieve it, they must find solutions. As unique solutions are rarely the case, social systems explore simultaneously multiple solutions and give place to trade-offs that enable organisms to exploit resources and to respond differentially to environmental pressures. These solutions can vary from apparently simple ones to those that appear more complex (Hobson et al., 2019).

As we discussed in the previous section, the existence of a tradeoff due to feedback loops between scales underlies organized complexity. For example, social animals can exhibit complex behaviors as organized societies if their genome is organized enough to enable the orchestration of all the genes responsible for that behavior. Animals’ complexity tradeoffs can also explain why some animals become adaptive while others become efficient (Siegenfeld and Bar-Yam, 2020).

Adaptability encompasses many independent actions taken in parallel (a situation in which the system is overly complex). On the other hand, efficiency occurs when many parts of a system manage to work in concert (Giving place to specialized systems). Because of the tradeoff between complexity and scale, an adaptable system can become more complex, but predominantly at smaller scales, while an efficient system will have a complexity profile with lower complexity but extending to larger scales (Siegenfeld and Bar-Yam, 2020).

Following the later statement, it is timely to rethink our current framework to classify social complexity, as it is now reasonable to say that solitary animals fit in the description of adaptability, while group-living animals appear as efficient systems. The key idea is that when speaking about complexity we must consider the scale. To this end, we cannot assert that a solitary animal is less complex than a group living organism; instead, we could say that they are both complex at different scales. This could help reconcile the lack of consensus in the definitions and findings throughout studies of social complexity. To prevent this from further happening, studies on animal social complexity should make explicit the scales at which social traits are being studied and measured.

7 CONCLUSIONS

Social complexity is a problem of organized complexity that must be approached as a multiscale phenomenon.

This approach considers multiple scales and interactions across components of the system and enables to study the phenomena as a whole. In our view, this way may get us closer to address questions such as: What is social complexity? Can social complexity be measured? Are some animals more socially complex than others? And if this is the case, why?

Social complexity studies are becoming more frequent, and a strong theoretical framework is needed to integrate new findings. We believe that a good approach is to work towards a theory of social complexity that integrates concepts of complex systems, behavioral ecology, and social systems.

Also, future animal social studies should include the molecular scale -e.g., the complexity of genome architecture- which allows comparing social complexity, within and between species, because this scale of organization is shared by all living organisms. Comparative genomics and systemic approached simulations might be helpful to answer the mentioned questions and to improve our understanding of social complexity.

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