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Stemming the flow: social evolution an information-infection trade-off

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Abstract:	In the midst of Covid-19, we are witnessing just how critical disseminating reliable information and social distancing are in limiting pathogen transmission. This article highlights how evolution has dealt with similar information versus pathogen spread trade-offs in animal societies. We encourage an integrated theory about how we envision social networks to emerge.

Strasbourg, the 01st of April 2020

<u>Cover letter</u>

Dear editor

We are submitting the manuscript: "*Stemming the flow: information versus infection in social evolution*" to be considered for publication in *Trends in Ecology and Evolution – Science & Society.*

The current pandemic caused by SARS-CoV-2 has raised a number of issues related to social strategies to avoid infection. Humans are trying to significantly downsize their physical contact networks to slow transmission, and this raises countless concerns given our reliance on an increasingly globalized world. We also speed up our information transmission through social media to find better solutions in the face of outbreak situations. Like humans, other group-living animals make decisions constantly that affect their social lives. Though other species cannot revolutionize their mechanisms of information exchange, as we do through digital means, they nonetheless use diverse communication modalities to spread information. According to socio-ecological pressures, individuals modify their contact rates and this has a scaling-up effect seen in the structure of the networks in which they are embedded. Individual decisions thus affect the contact network, which in turn affects the probability of an individual acquiring a pathogen. This is what humans are trying to optimize when fighting pandemics.

In this article, we explore recent advances in the field of social transmission in animal societies and propose an integrated theoretical framework through which to investigate an under-researched evolutionary trade-off facing all social animals: how to maximize information gains while minimizing pathogen acquisition. Such a framework can help us understand the evolution of social structure under competing selection pressures and may provide insight into the design and/or implementation of health interventions. We believe this topic is suitable for the section Science & Society because it addresses a highly important subject in the midst of today'S Covid19 Pandemic. The thematic of study is of interest to a broader audience, including behavioural ecologists, network scientists, epidemiologists, general community etc.

The manuscript has been written to appeal to a broader audience of non-specialists by avoiding jargons (whenever possible). All authors are aware that the manuscript has been submitted for publication and have agreed on its content.

We thank you for considering our manuscript for publication in *Trends in Ecology and Evolution – Science & Society*, and we look forward to hearing from you soon.

Sincerely yours,

Valéria Romano, Andrew J.J. MacIntosh, Cédric Sueur

Stemming the flow: Information, Infection, and Social Evolution

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Keywords

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Abstract

In the midst of Covid-19, we are witnessing just how critical disseminating reliable information and social distancing are in limiting pathogen transmission. This article highlights how evolution has dealt with similar information versus pathogen spread trade-offs in animal societies. We encourage an integrated theory about how we envision social networks to emerge.

Introduction

> "It is certain that either wise bearing or ignorant carriage is caught, as men take diseases, one of another: therefore, let men take heed of their company". Shakespeare, Henry IV, part 2 (1600)

As William Shakespeare observed, the contacts that individuals make lead to the passage of information among them, for better or worse, just as it does for the agents of disease. The current SARS-CoV-2 pandemic has brought into focus numerous social mechanisms to mitigate transmission. Social customs like handshaking have become anathema, while digital communications are now preferred over in-person meetings. Ultimately, humans must significantly downsize their physical contact networks to slow transmission, and this raises countless concerns given our reliance on an increasingly globalized world.

Like humans, other group-living animals make decisions constantly that affect their social lives, such as whether or not to interact with a particular group mate. Though other species cannot revolutionize their mechanisms of information exchange, as we do through digital means, they nonetheless use diverse communication modalities to spread information. According to socio-ecological pressures, individuals modify their contact rates and this has a scaling-up effect seen in the structure of the networks in which they are embedded. Individual decisions thus affect the contact network, which in turn affects the probability of an individual acquiring a pathogen. This is what humans are trying to optimize when fighting pandemics. The field of biomimetics has produced invaluable solutions to myriad systemic and engineering challenges [1], but is there scope to use animal behavior research in search of solutions to promote global health?

In this article, we explore recent advances in the field of social transmission in animal societies and propose an integrated theoretical framework through which to investigate an under-researched evolutionary trade-off facing all social animals: how to maximize information gains while minimizing pathogen acquisition. Such a framework can help us understand the evolution of social structure under competing selection pressures and may provide insight into the design and/or implementation of health interventions.

The trade-off between information and pathogen transmission

Diversified patterns of social interaction are reflected in population-level outputs such as information and pathogen transmission. For example, the number and strength of social interactions affect how fast information and/or a pathogen is transmitted through a population. This leads to an evolutionary trade-off: while social relationships facilitate the transmission of information (e.g. behavior, knowledge), they also favor the spread of socially-acquired pathogens (e.g. respiratory viruses, ectoparasites) [2]. Fine-scale details of these social interactions, i.e. as revealed by social network analysis (SNA), can help us understand how individuals deal with the challenges of group-living.

Network metrics are statistical measures used to characterize properties of the network, such as an individual's position within its network of contacts and the characterization of the network as a whole, or its topology. Through SNA, researchers have discovered that network properties fluctuate in time with the accumulation of individual decisions. Depending on circumstance, informed individuals might find themselves in a more central position within a network [3], while individuals avoiding contact with others showing signs of sickness might instead contribute to a more subdivided, and thus less connected, network [4]. Such behavioral and network plasticity ultimately determines the structure of information and pathogen exchange, and is thus a critical component of the resilience of populations to socio-environmental challenges. With this in mind, in Box 1 we propose an integrated framework for understanding emergent social structure given the competing demands of information acquisition and pathogen avoidance, while offering some examples of pathogen control among social animals in Box 2 and in the next section.

Mechanisms of social avoidance

The relationship between sociality and infectious disease is, on the surface, straightforward: animals living in closer proximity and with higher contact rates should experience higher rates of pathogen transmission. However, species have evolved myriad defenses to prevent and/or respond to pathogen invasions. These anti-parasite strategies have been collectively termed the '*ART of pathogen handling*': avoidance, resistance, tolerance [5]. To complement immunological defenses, behaviors such as hygiene, self-medication and social avoidance have evolved, the latter of which, as humans are currently experiencing through worldwide lockdowns, may be among the most important mechanisms of '*social immunity*' [6] and other forms of behavioral immunity preventing pathogen transmission [7].

Mechanisms of avoidance, however, may vary. Individuals may actively self-isolate, or due to their own lethargy may engage in fewer social interactions as part of a generalized sickness response. Uninfected individuals may also actively avoid infected conspecifics, especially those showing signs of sickness. Isolation of the infected may even be imposed or enforced by others. But whatever the case may be, restricted social interaction impacts social structure in ways that down-regulate social transmission and reduce a pathogen's basic reproduction number (R_0) to below replacement (R_0<1), after which point the outbreak becomes unsustainable.

Examples of social avoidance in animals are widespread, in taxa as divergent as arthropods and mammals (Box 2). One poignant example seen in the black garden ant (*Lasius niger*) demonstrates that pathogen exposure induces behavioral changes that reinforce transmission-inhibitory characteristics in the contact network: i.e. increased modularity, clustering and assortativity, and decreased transmission efficiency [4]. Not only did foragers exposed to a fungus natural to the ants' habitat isolate themselves from the colony, healthy foragers also decreased their contact time with the rest of the colony [4]. If this sounds familiar, it is because it is: humans around the world are currently using the same approach to COVID-19.

The ant example highlights that social animals are capable of modulating their behavior in ways that increase the benefits and avoid the costs of social interactions dynamically, and this should lead to detectable changes in network structure, which in itself up- or down-regulates social transmission (Figure 1). But how are individuals expected to behave when, despite the risks of infection, there remains the need to acquire social information? While empirical studies in animals are lagging, a recent theoretical model of roost selection in bats has demonstrated that fission-fusion behavior, whereby individuals fluctuate in their degree of sociality through time, resulting in more or less modular networks, is a strategy that can result from a collection of individual decisions aimed at maximizing information accuracy and minimizing infectious disease risk [8]. Collectively, network properties like modularity and density can be used as powerful estimators of transmission processes, with each property potentially working as a buffer and/or facilitator of social transmission.

(Figure 1)

The evolutionary mechanisms of social transmission

Social networks have self-organizing components in their local interactions and individual behavior, which remain flexible and responsive to the divergent pressures each individual face. Humans know this and try to use this information to manage network flows in myriad contexts. The mechanism by which individual behavior influences the social network into which they are embedded is known as "*collective social niche construction*". Social networks are demonstrably dynamic, and interaction costs and benefits cause variation in individual decisions about with whom and how frequently to interact. The emergent social structure observed then feeds back into the dynamics of social transmission. From this perspective, individuals that better adjust their behaviors to meet the challenges both external to and inherent in social relationships might be able to increase their own fitness (i.e. survival and reproductive success). These individual traits would then be favored by natural section, and the social networks they form will have gained resilience through evolutionary time.

Prognosis

Illuminating the role of individuals, as they navigate their social worlds and contribute to the various flows within their respective social networks, highlights that effective epidemic control strategies depend on the collective sum of their behavior. We have shown that solutions do exist in social animals, and that, like in humans, other species can adapt their contact rates, their communication modalities and their network structure to limit pathogen spread. Our modern understanding of pathogen spread and its mitigation has a history of less than two centuries, whereas evolution has used hundreds of millions of years to hone solutions to this critical challenge in nature. More attention on this topic is needed, on a greater diversity of species and on the underlying mechanisms of network plasticity and resilience. In this context, we call for more research into the information-pathogen trade-off in network evolution among social animals. Such research may reveal novel solutions to infectious disease outbreaks with relevance even to human social systems. We propose that consideration not only of how infectious diseases emerge in animal populations but also how they are regulated and even mitigated through processes like those described in this essay is well within the purview of the One Health paradigm, and may thus contribute to the fostering of global health and well-being.

Beyond our social world

Perhaps one of the least controversial lessons we have learned during the COVID-19 pandemic, yet one that has garnered far less media attention since the world shifted into lockdown of human interaction, is that, for better and for worse, our own social networks are situated within a broader ecological context of interaction with nature. As the onrushing of human consumption invades deeper and deeper into the wild places of the world, we are increasingly exposed to all manner of novel infectious organisms that circulate undetected in wildlife. It is common knowledge that most emerging infectious diseases in human populations are zoonotic, i.e. of animal origin, with as much as 70% of those originating in wildlife [9]. Social distancing and digital communication can slow the spread of SARS-CoV-2, but more responsible interaction with the natural word [10] might have mitigated its emergence altogether.

Box 1. At the interface of social transmission and social structure

Hinde's framework of animal society [11] posits that the quality and patterning of relationships is molded by social structure, while social structure itself is driven by socio-ecological factors. Cantor & Whitehead [12] extended Hinde's framework by incorporating information transmission at the final level of the model shown in Figure BI, highlighting bidirectional effects. For example, variation in the vocal repertoires of cetaceans causes clustering of individuals with similar patterns [13]. Within clusters, individuals are also more likely to share information.

What remains missing from Hinde's framework, however, is a role for deleterious forms of social transmission like those that lead to infectious disease. Socially-transmissible pathogens may negatively affect social cohesion, either directly or indirectly, by reducing social connectivity. Concurrently, the overarching social structure sets the conditions under which individuals are exposed to such pathogens, creating bidirectional feedback (Figure BI). Here, we extend Hinde's framework to incorporate connection costs like the spread of pathogens (Figure BI). Instead of considering transmission as an endpoint, or assume that information flow is all that matters, we suggest simultaneous examination of information and pathogen transmission as explicit and opposing entities driving social structure and behavior. The result is a classical fitness trade-off in which the need to exploit social relationships while minimizing the associated costs drives the evolution of social behavior.

(Figure BI)

Box 2. Examples of social avoidance behaviors across the animal kingdom

Evolved strategies other than the physiological immune system allow social animals to combat the spread of infection, such as conspecific avoidance. Examples of social avoidance and self-isolation abound in nature (Figure BII). Caribbean spiny lobsters (*Panulirus argus*) avoid dens housing individuals infected with a lethal virus [14]. Immune-challenged mice (*Mus musculus domesticus*) reduced their own rates of social contact by avoiding encounters with group members [15]. Trinidadian guppies (*Poecilia reticulata*) avoid conspecifics infected with an ectoparasite in the late stages of infection [16]. Mandrills (*Mandrillus sphinx*) recognize parasitized conspecifics and avoid grooming contaminated body regions [17]. Critically, mandrills appear not to avoid interactions with infected maternal kin [18]. This last discovery should resonate with those taking risks to make quarantine with family. Social insects go so far as to engage in collective defense against parasites through so-called '*social immunity*', where they cooperate in different ways to combat colony infection [6]. These examples emphasize how social behavior can influence the dynamics of pathogen transmission via an added layer of defense.

(Figure BII)

Acknowledgments

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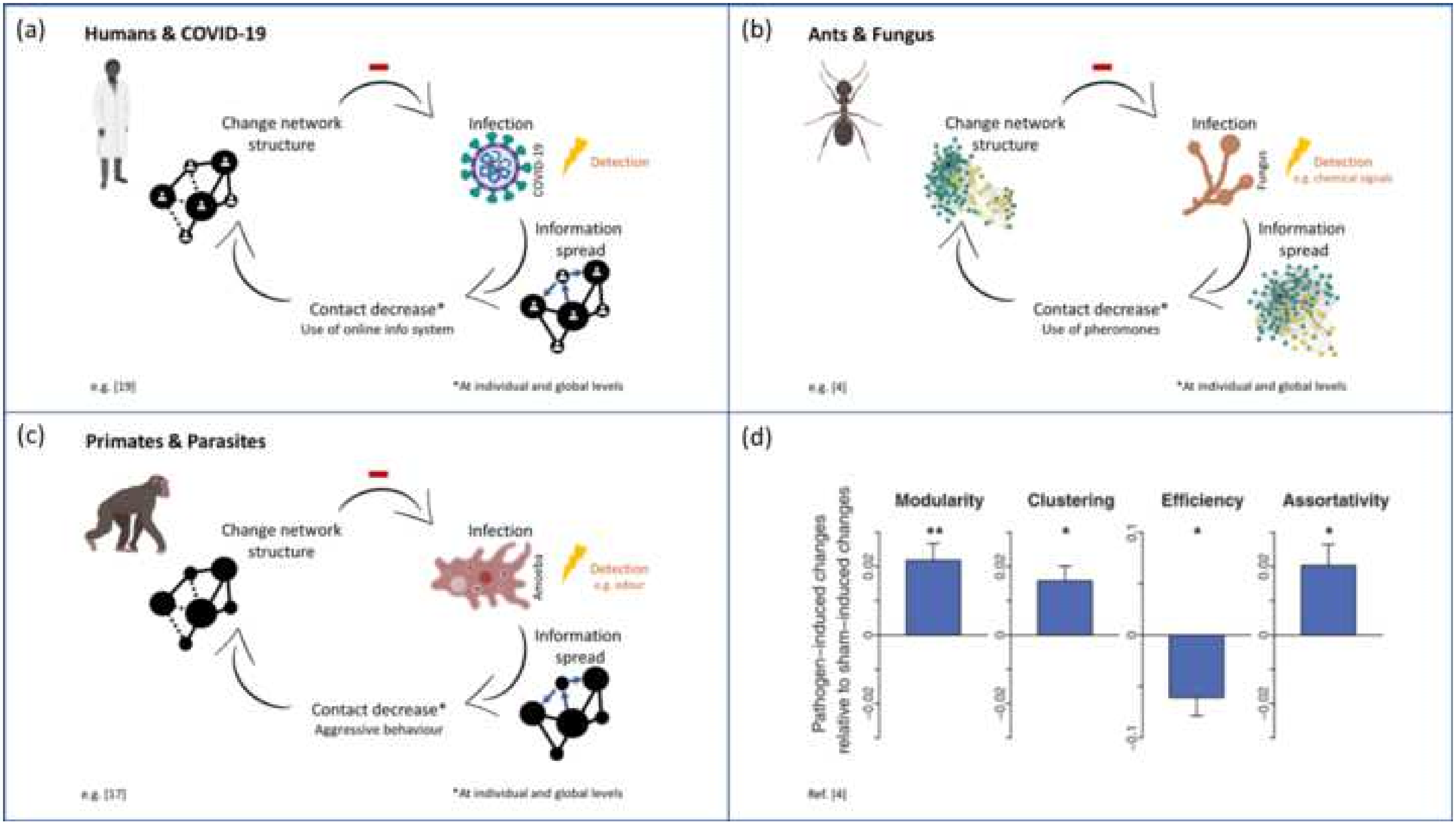
Figures legend

Figure 1. Evidence for network plasticity and its effects on pathogen transmission rates. We present the behavioral mechanisms underlying human (a), ant (b), and non-human primate (c) social contact. When a pathogen is introduced in a system and detected, infected and non-infected individuals usually change their contact rates. This leads to changes in network structure, such as increasing the number of subgroups, which affects the efficiency of pathogen transmission (d). Conceptually, the feedback is similar across the three systems depicted. The communication system can also change, as exemplified by both ants and humans, from a targeted and local contact-based modality to a global or more broadly-disseminated modality (e.g. public information such as online communications or pheromone trails/clouds). The networks in (b) and graph in (d) were reprinted from Stroeymeyt et al. 2018 'Social network plasticity decreases disease transmission in a eusocial insect', *Science* 941–945. Copyright (2018), with permission from the American Association for the Advancement of Science. Images from macro and microorganisms created with BioRender.com.

Figure BI. Schematic representation of the feedback loop between social structure and social transmission, both beneficial and detrimental. Individual behavior leads to different patterns of social interaction, which in turn influence and are influenced by cultural and pathogen transmission pressures. We propose a framework that integrates the two, simultaneously examining information and pathogen flow as explicit and opposing entities, with emergent network properties reflecting a trade-off between them. Macaque images, credit: Delphine Vaufrey.

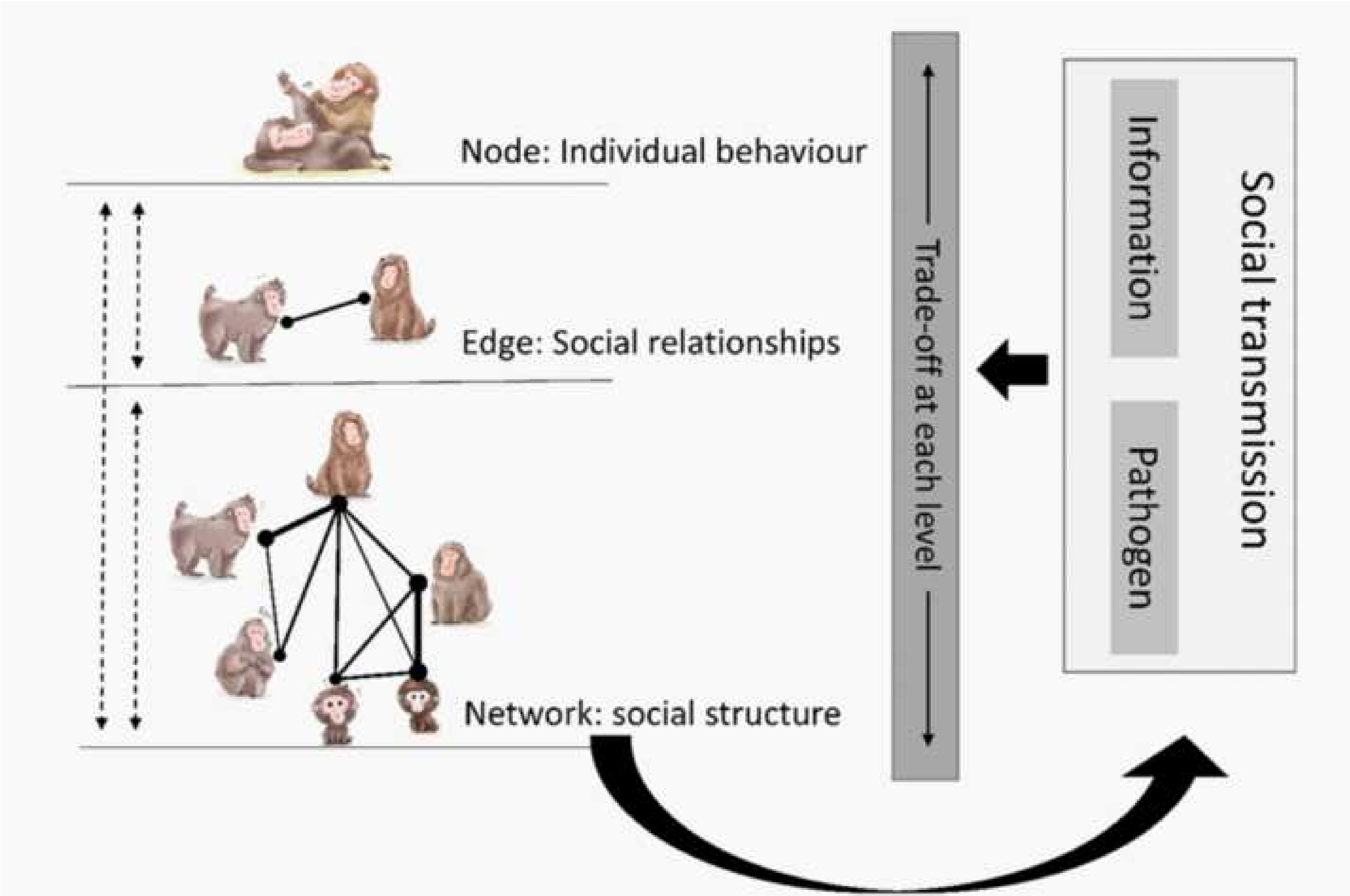
Figure BII. Empirical studies demonstrating that social avoidance is an important strategy for controlling pathogen spread: (a) Trinidadian guppies (*Poecilia reticulata*) (credit: Darren Croft), (b) mandrills (*Mandrillus sphinx*) (credit: Paul Amblard-Rambert), (c) Caribbean spiny lobsters (*Panulirus argus*) (credit: Donald Behringer) and (d) house mice (*Mus musculus domesticus*) (credit: Barbara Koenig).

Figure1


(a)
Humans & COVID-19
Change network structure
Infection
COVID-19
Detection
Information spread
Contact decrease*
Use of online info system
e.g. [19]
*At individual and global levels
(b)
Ants & Fungus
Change network structure
Infection
Fungus
Detection
e.g. chemical signals
Information spread
Contact decrease*
Use of pheromones
e.g. [4]
*At individual and global levels
(c)
Primates & Parasites
Change network structure
Infection
Amoeba
Detection
e.g. odour
Information spread
Contact decrease*
Aggressive behaviour
e.g. [17]
*At individual and global levels
(d)
Modularity
Clustering
Efficiency
Assortativity
**
*
*
*
Pathogen−induced changes relative to sham−induced changes
0.02
0
-0.02
0.1
-0.1
Ref. [4]

FigI-Box1

Click here to access/download;Figure;FigI_Box1.png



FigII-Box2 Click here to access/download;Figure;FigII_Box2.png