Quality, quantity, and the adaptive function of social relationships

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1. Social relationships: key predictors of individual fitness

Social interactions are an integral part of animal life. Rather than interacting with conspecifics at random, individuals from many species have specific partners they sleep near, travel, feed, groom, preen, huddle with and vocalise to [1, 2]. From those repeated affiliative, or friendly, interactions emerge affiliative relationships [hereafter "**social relationships**", see Glossary; 3]. Together, those relationships result in a complex **social network** that shapes how individuals experience their day-to-day environment, influencing their ability to obtain food, avoid predators, attract mates, and care for their young [3-5]. It is therefore not surprising that social relationships are a key predictor of individual fitness, consistently emerging as having strong effects on survival and reproductive success across a variety of taxa [6-10].

This link to fitness proxies underscores that social relationships are evolutionarily adaptive. Yet, a major question remains: Why exactly do social relationships help individuals? What do well-connected individuals obtain from their social partners that allows them to survive and reproduce to a greater extent than their less socially connected counterparts? While individual studies have begun to shed light on the potential pathways linking social relationships to fitness benefits, consolidating these findings and identifying general trends in the adaptive function of social relationships has proven challenging [7, 11]. This difficulty stems from two interrelated issues: (1) the multitude of potential pathways linking social relationships to fitness [7, 12] and (2) the diversity of social relationships that can be formed [10, 13-15]. A framework integrating these two issues is needed to guide systematic research and reveal broad patterns in the adaptive function of social relationships. To this end, we draw on two well-established approaches – socio-ecological theory, which provides predictions for pathways linking sociality to fitness, and network science, which provides concepts and tools to quantify social connections – to put forward the Adaptive Relationships Framework.

2. A socio-ecological approach to revealing the pathways linking social relationships and fitness

Socio-ecological theory provides a solid foundation from which to make sense of the multiple potential pathways linking social relationships to fitness. Socio-ecological models examine how social and ecological risks and resources shape **social organisation**, **social structure** and mating and care systems, the core components of social systems [1, 16]. These models have led to significant advances in our understanding of the evolution of social processes, including group-living, dispersal patterns and the distribution of reproduction [17].

Yet, while the socio-ecological basis for variation in social organization and mating systems has been studied extensively [4, 18-24], less attention has been given to social structure (i.e., the patterning of

social interactions among individuals). One clear exception can be found in nonhuman primates where social relationships among females are hypothesised to be shaped by competition over food and the risk of predation and infanticide [25-29]. Extending this primate-specific model to a wider range of taxa and socio-ecological pressures could yield significant insights, as many species (whether obligatorily social or not [2, 30]) form social relationships, which are ultimately shaped by their social and ecological contexts.

In the Adaptive Relationships Framework outlined below, we use principles derived from socio-ecological theory to categorize the types of challenges animals face that can be resolved using social relationships. First, however, we address the issue that animals form different types of social relationships.

3. Relationship quality and quantity – network science and two fundamental dimensions of social relationships

The second challenge to revealing the adaptive function of social relationships is the diversity of relationships that individuals can form. Social network science is particularly useful in this context, as it provides a structured way to examine the different types of relationships that exist and the benefits they offer. One of the most influential theories in this field posits that relationships of different strengths—strong bonds and weak ties—serve inherently different functions that can only be fully understood when considered within the context of the broader social structure [31]. Strong bonds are reliable partnerships that provide critical support, while weak ties act as bridges to the broader social network, facilitating access to resources and information. This idea that weak ties can serve an alternative but equally important function as strong bonds, also referred to as the "strength of weak ties" has been pervasive in human behavioural and network sciences. More recently it has begun to take hold in behavioural and evolutionary ecology [14, 32, 33], with growing recognition that animal social relationships range from strong, lifelong bonds with a few partners, to weaker, more transient ties that connect individuals more widely within their social networks [13, 34].

Beyond representing strong and weak ties [31], we propose that these different types of relationships reflect differences in how individuals prioritize and invest their **social effort**. Specifically, the diversity in social relationships essentially revolves around two key factors: how an individual allocates its social effort among potential partners and the level of investment an individual makes in each of its partners. These factors result in two fundamental dimensions of social relationships: **relationship *quantity***, an individual's number of relationships and how integrated they are in the wider social network, and **relationship *quality***, the relative strength and stability of each of their relationships (Box 1).

Box 1: What are relationship quality and quantity?

Intuitively, relationship quantity is simply the number of social relationships an individual has, and relationship quality is the strength of those relationships. But when thinking about them in a network perspective, it is a bit more complex than that.

Specifically, one key feature of relationship quantity is not just that individuals have many social partners, but also the resulting indirect connections that emerge from those relationships, which ultimately facilitates better

integration in the overall social network [35-37]. Indeed, the "strength of weak ties" idea was proposed to encompass exactly those elements – that is, weak ties yield benefits because they allow individuals to be better connected to individuals in the network other than their direct social partners [31].

Relationship quality is also more than just the strength of social relationships. There are other important components of social relationships that define their quality, including their stability, predictability and interdependence, all of which require repeated interactions over time to develop [34, 38-41]. In addition, it is not the absolute strength of relationships that determines their quality, but their *relative* strength (Fig. 1 & 2): quality relationships are those that are stronger, more stable, and clearly differentiated from an individual's other relationships, reflecting selective investment in a few preferred social partners [7, 42, 43].

The biological significance of relationship quality and quantity is supported by empirical results linking these two dimensions to fitness proxies across taxa [8]. For example, individuals with more connections or who are better indirectly connected to their networks live longer in some species [44-46], while individuals with strong and stable relationships live longer in others [47-49]. Comparative research across species further confirms measures of relationship quality and quantity are often only moderately, or even negatively, correlated [13, 14, 32, 50], suggesting that they represent two distinct dimensions of an individual's social network. A key question we now need to address is what selective pressures favour relationship quality or quantity.

Here, we unify the idea that social relationships vary along dimensions of quality and quantity with classic socio-ecological theory to create a framework of testable predictions for the adaptive function of social relationships (Fig. 1). The Adaptive Relationships Framework outlines the broad socio-ecological pressures that animals face, identifies the social needs that arise from these pressures, and puts forward testable predictions for the social strategies and emergent structures that help animals overcome these challenges.

4. The Adaptive Relationships Framework

The Adaptive Relationships Framework proposes that different environments select for individuals to prioritize the quality or the quantity of their relationships. Depending on the environmental challenges they face, animals require different **social solutions** to cope effectively, such as coalitionary alliances or access to social information. To access these solutions, they need to adopt distinct **social strategies**: either strengthening bonds with a few key partners (prioritizing relationship quality) or expanding their network to include many connections (prioritizing relationship quantity; Fig. 1). Relationship quality may therefore be selected when a few strong and reliable partnerships are needed, while relationship quantity is favoured when the number of relationships and connections to the wider network matter more than relationship strength or the identity of specific partners. We expand on the discrete steps of this framework below and provide example case studies in support of these ideas.

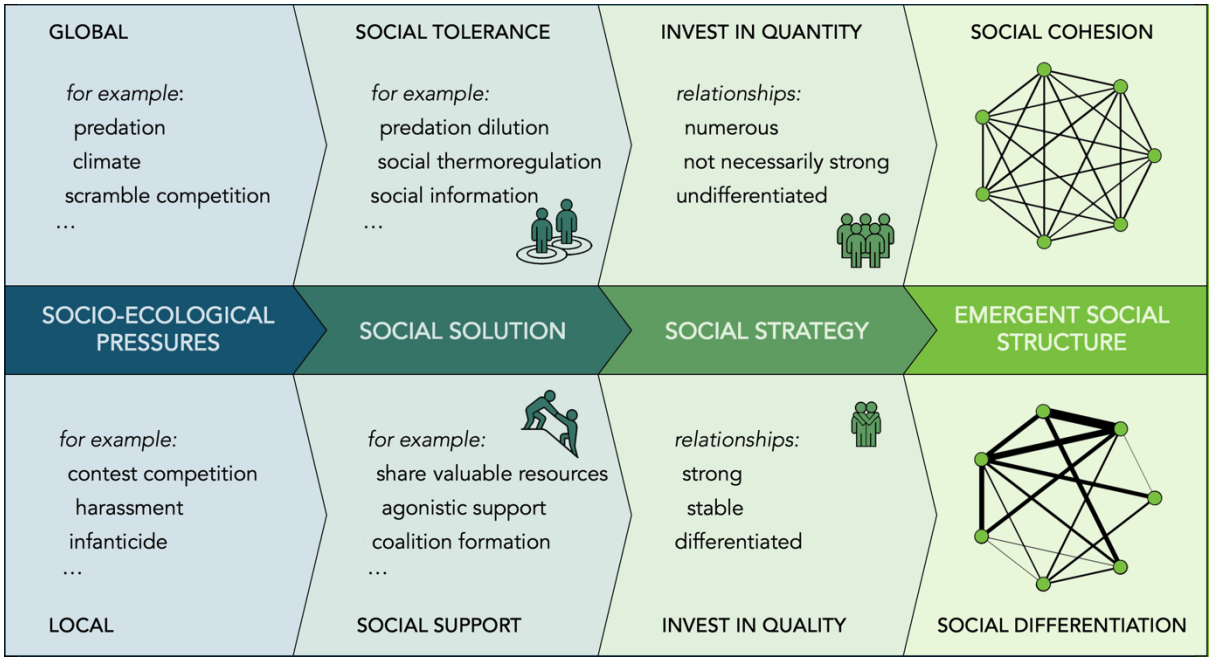

Fig. 1: **The Adaptive Relationships Framework**. We propose that socio-ecological pressures create specific social needs in animals, driving them to adopt different social strategies and resulting in diverse social structures. Animals that experience pressures manifested at a global scale, including harsh climate and predation, require tolerance in their social environment and are predicted to invest in a social strategy characterised by its *quantity*, maximising the number of others they are connected to and resulting in cohesive and non-modular social structures. Animals that experience pressures manifested more locally, such as contest competition amongst group mates, require support from their social partners and are predicted to invest in a social strategy characterised by its *quality*, investing in a few strong and stable relationships with specific others and resulting in highly differentiated social structures. Although these pathways are presented as distinct, they exist on a continuum (Fig. 2): pressures are often not strictly local or global and animals frequently encounter multiple socio-ecological challenges at once, requiring them to balance diverse social solutions and strategies.

From socio-ecological pressures to social solutions: Do you need social tolerance or social support?

Ultimately, social relationships are adaptations that provide animals with solutions to cope with pressures in their environment, which can be broadly categorised as being global or local (Fig. 1). Global pressures, such as climate and predation, impact entire groups or populations relatively uniformly. That is, all individuals are exposed to the cold and are at risk of predation. These pressures are best addressed by **social tolerance**, allowing individuals to remain close to others and move freely within their social environment.

Global pressures have long been recognized as key evolutionary forces that drive animals to group together, whether in fluid, temporary aggregations or stable social groups [21, 51, 52]. What we propose here is that, even within these aggregations, animals who are better tolerated by their group members gain advantages in facing these pressures. For instance, social tolerance offers safety in numbers, mitigating the risk of predation [53]. Redshanks (*Tringa totanus*) at the margins of flocks are more likely to be targeted by sparrowhawks [*Accipiter nisus*; 54], and vervet monkeys (*Chlorocebus pygerythrus*) that are more integrated into their social networks experience lower predation risk, benefiting from both reduced vigilance and increased foraging time [55].

Social tolerance also offers advantages in scramble competition, an indirect form of competition where individuals aim to exploit resources before others [56]. In such contexts, tolerance from social partners allows individuals to feed together on non-defendable resources with minimal conflict. Female plains zebras (*Equus burchelli*) and eastern grey kangaroos (*Macropus giganteus*), for example, co-feed peacefully in groups due to high social tolerance [57, 58]. Additionally, social tolerance enhances foraging efficiency by reducing vigilance and facilitating the sharing of social information about resource availability and opportunities to detect or exploit food [59]. For instance, small passerine birds (family *Paridae*) who are more central in their social networks are more likely to locate and exploit novel foraging patches than less central individuals [60].

Tolerance can also help animals cope with climatic conditions through social thermoregulation [61]. Walrus (*Odobenus rosmarus*) calves and females tend to position themselves in the most central parts of the herd, where they benefit from greater protection against both the cold and predators [62]. Barbary macaques (*Macaca sylvanus*) form larger huddles during cold winters [63], which increases their chances of survival [45]. Similarly, rhesus macaques (*Macaca mulatta*) cope more effectively with extreme heat by tolerating each other in shaded areas [64].

Local pressures, on the other hand, arise at the level of individual interactions within the social system and affect individuals differently. Those pressures, such as contests over monopolizable resources, harassment and exposure to socially transmitted pathogens, are key costs of grouping together and the presence of others. Rather than having many partners, addressing local pressures requires **social support** to help individuals navigate conflicts and competition with others in the group.

Social support plays a crucial role in contest competition, where individuals directly compete for valuable, defendable resources like clumped food, mates, or territory [56]. In such contexts, receiving social support in the form of alliances or coalitions can greatly improve an individual's chances of securing valuable resources [65, 66]. For example, male bottlenose dolphins (*Tursiops aduncus*) form stable, long-term alliances to defend females from rivals (Box 2), and grey wolves (*Canis lupus*) share meat with their social partners [67].

Social support not only directly facilitates resource acquisition but also helps individuals achieve and maintain higher dominance rank, which can further improve their priority of access to resources [68]. Common ravens (*Corvus corax*) selectively support their social partners in conflicts, increasing both their own and their partners' positions in the dominance hierarchy [69]. Additionally, social support in agonistic encounters can mitigate the costs associated with competition. In rhesus macaques, for example, social support reduces the risk of potentially fatal injuries during conflicts [70].

Social support also offers protection against threats like harassment, infanticide, and conflicts with rival groups. Female feral horses (*Equus caballus*) experience less harassment from males when they receive social support from other females [71], and female African lions (*Panthera leo*) form coalitions to defend their cubs against infanticide by intruding males [72]. In banded mongooses (*Mungos mungo*), entire groups collectively engage in risky intergroup conflicts over food and mates [73]. Similarly, in chimpanzees (*Pan troglodytes verus*), close social partners support each other in intergroup conflicts, risking serious injury or even death to do so [74].

Finally, social support can take the form of engaging in sickness behaviours, such as grooming social partners to remove pathogens or providing food to sick partners [75, 76]. For instance, mandrills (*Mandrillus sphinx*), banded mongooses and vampire bats (*Desmodus rotundus*) will continue to groom their closest social partners, even when they are infected [77-79]. In grey wolves, the cost of infection can be mitigated by the presence of social partners, likely because sick individuals still get to eat even when they are unable to contribute much to the hunt [80].

From social solutions to social strategies: Do you need relationship quality or quantity?

To gain access to social tolerance or social support individuals need to adopt distinct social strategies (Fig. 2). For social tolerance, mutual benefits typically arise from the mere presence of others [81]. Individuals therefore do not need close or even differentiated relationships with specific others, but rather benefit from spreading their social effort across a broader network of tolerant partners. For example, female yellow-bellied marmots (*Marmota flaviventer*) with a greater number of social partners delay their flight response to predators [82], and have decreased summer mortality, which is primarily caused by predation [83]. Male killer whales (*Orcinus orca*) with a greater number of social partners have higher survival rates during food-scarce years [44], likely due to their ability to access social information about where to find salmon [84].

In contrast, social support involves partners taking significant risks for one another, such as providing active support in conflicts at the risk of personal injury, sharing valuable resources that could be kept for themselves, or increasing personal disease exposure by engaging with sick individuals [85]. Such high-risk behaviours require stronger incentives to motivate individuals to incur these costs [86]. Here, strong and stable relationships are essential because they create fitness interdependence between social partners [38, 87]. As individuals invest in their relationship, they gradually build consistency and predictability, or 'mutual trust' [40, 88]. This reduces the risk of partner defection and increases the likelihood that support will be reciprocated in the future [38, 87]. For example, vampire bats will regurgitate blood to feed hungry roost-mates, but only perform this high-cost behaviour towards social partners with whom they have developed strong enough relationships [89]. Over time, social partners' fates become increasingly interconnected, motivating ongoing support [39]. For instance, female hyenas (*Crocuta crocuta*) and male Assamese macaques (*Macaca assamensis*) form coalitions with their closest allies to challenge higher-ranking individuals, increasing their own dominance rank and ultimately enhancing their reproductive success [43, 90-92]. Without continuous mutual support, both partners would lose their social status and the associated benefits.

We therefore predict that global pressures select for individuals who form social relationships (of any strength) with many other individuals – a social strategy that prioritizes investing in relationship quantity. In contrast, in contexts of localised socio-ecological pressures, individuals need to develop strong, stable social relationships with a few, preferred partners – a strategy of investing in relationship quality.

From social strategies to social structure: The emergence of cohesive or differentiated networks.

Selective pressures acting at the level of the individual also scale up to impact social structure at the group or population level [3, 35, 93]. Socio-ecological pressures that select for social tolerance through relationship quantity will give rise to **cohesive**, non-modular social networks. In those networks, most

individuals are connected to each other through relationships that are relatively similar between all pairs. For example, rock hyraxes (*Procavia capensis*), which are vulnerable to predation and rely on social information to navigate their fragmented habitat, have higher survival rates when living in cohesive networks with weakly differentiated relationships [94].

Conversely, pressures that require social support through the formation of high-quality relationships will result in networks that are less cohesive, more differentiated and modular. In these networks, some pairs have strong connections, while others may only be weakly or indirectly connected, if at all. For example, female chacma baboons (*Papio hamadryas ursinus*), which form long-term cooperative alliances to maintain rank and access resources, have highly differentiated networks. In those networks, individuals focus most of their social time on a few strong relationships [95], and it is the strength and stability of those relationships that link to longevity [47].

These social structures are not just emergent properties of pairwise relationships, but also have their own benefits. For example, higher network cohesion facilitates more effective collective action [96, 97] and faster spread of information [98], while greater network differentiation and modularity slow the transmission of socially transmitted pathogens [99].

Box 2: Testing the Adaptive Relationships Framework

We have outlined evidence supporting each step of the Adaptive Relationships Framework. However, comprehensive testing of the framework requires evidence across all steps, along with the fitness consequences of the social strategy or structure in question. Although rare, evidence from some systems span most steps of the framework.

Male bottlenose dolphins in Shark Bay compete for access to females [100]. According to the Adaptive Relationships Framework, the social solution to this local pressure is social support, and males should invest in relationship quality. In line with this, male bottlenose dolphins form strong, long-term bonds with a few partners [101], with whom they herd females [102], resulting in a highly differentiated social structure [103], where relationship quality predicts reproductive success [104]. Across bottlenose dolphin populations, male alliances are more common at higher densities, further supporting the idea that competition drives the need for quality relationships [100, 105]

I. Two bottlenose dolphins

Female Masai giraffes (*Girafa camelopardalis tippelskirchi*) must locate food on the dry Tarangire savannah [106]. According to the Adaptive Relationships Framework the social solution to this global pressure is social tolerance, and females should invest in relationship quantity. In line with this, female giraffes who associate with a greater number of other females experience higher survival, while those with strong relationships do not [46]. Relationship quantity likely allows for shared habitat use or access to information about food availability, although there is no direct evidence for this yet.

II. A group of Masai giraffes

Quantifiable changes in socio-ecological pressures also provide natural experiments to test the Adaptive Relationships Framework. For example, female rhesus macaques on Cayo Santiago typically rely on strong social bonds to navigate contest competition over resources, with relationship quality predicting lower injury risk and higher survival [13, 70]. However, a major hurricane drastically altered their environment, increasing the need for access to shade. In response to this newly important global pressure, individuals expanded their networks to have a larger number of weaker ties [107] and relationship quantity, not quality, predicted survival [64].

III. Rhesus macaques sharing space in the shade

Comparing across populations that face different socio-ecological pressures is another way to test the Adaptive Relationships Framework. While comparative research on social relationships has been hindered by challenges in compiling, standardizing and analysing cross-species data [108], these issues are increasingly being addressed by methodological advancements [109, 110] and collaborative efforts to build comparative social databases [110-112]. These initiatives are bound to yield insights into the ecological and evolutionary drivers of social relationships.

It's more complicated, of course

We have thus far presented a framework that is a simplified version of reality—where groups or populations face a single socio-ecological pressure, need the corresponding social solution, which in turn determines the social strategy that individuals adopt and the resulting structure of their society. In reality, populations often face multiple pressures simultaneously [17], and within these populations, individuals may experience different pressures or encounter the same pressures to varying degrees based on factors such as their age, sex, and reproductive status [32]. Moreover, socio-ecological pressures can be dynamic, shifting in predictable or unpredictable ways over time [113-115].

Social solutions also exist on a continuum, reflecting the gradients of socio-ecological pressures to which they respond (Fig. 2). For example, while there are clear cases of scramble feeding competition– where relationship quantity provides social information and tolerance around non-defendable food patches [44, 58, 116] – and clear examples of contest competition – such as defendable prey carcasses that require social support and quality relationships [117, 118] – there are also food resources that are partly but not wholly defendable. In these cases, we may expect selective tolerance of a few close partners – a midway point between quantity and quality [119-121]. Similarly, dealing with predation ranges from predator dilution, which requires only social tolerance, to strategies that require more active social support to mob and repel predators [122, 123].

The social strategies outlined in this framework are also not entirely distinct, and social relationships often provide access to both social tolerance and support to some extent. By investing in quality relationships individuals still maintain a network of partners that tolerate them [13, 124], and while focusing on the quantity of relationships might initially result in a large number of weak connections, these can serve as the pool from which strong relationships may be built [125, 126]. Finally, networks aren't simply cohesive or differentiated, but instead most networks carry signatures of both cohesion and differentiation [127, 128]. We therefore expect individuals in most species to form both strong

and stable quality relationships as well as several weaker, more ephemeral ones connecting them more widely to their network. But within that general pattern, we predict that the constellation and magnitude of the socio-ecological pressures faced will tip the balance between individuals prioritizing quality or quantity (Fig. 2).

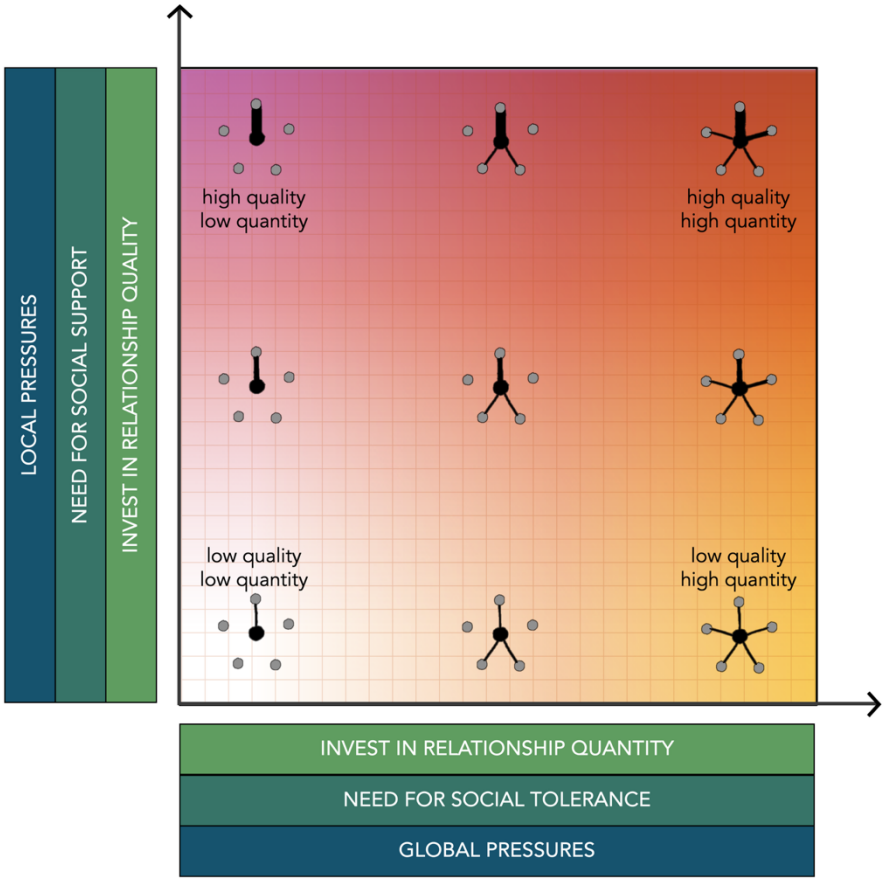

Fig. 2: Socio-ecological pressures and their corresponding social solutions and strategies exist on a continuum. Socio-ecological pressures are typically not strictly global or local but instead vary continuously from more global to more local. Consequently, the social solutions and strategies predicted by our framework (Fig. 1) also fall along a continuum. Each network in this figure represents an individual (central black node) and its potential social partners (grey nodes). The connections represent social relationships, where thicker lines represent stronger relationships. The heat map illustrates three points: 1) as the extent to which individuals face local pressures (y-axis) increases, individuals' need for high-cost, high-risk social support from their social partners goes up and they should increasingly invest in relationship quality; 2) as the extent to which individuals face global pressures (x-axis) increases, individuals need more social tolerance and should increasingly invest in the quantity of their relationships; and 3) when individuals face both global and local pressures, they should invest in both the quality and quantity of their relationships accordingly (top right of figure). Note that increasing relationship quality does not simply mean that individuals strengthen all their social relationships, but rather that they increase the relative investment of their social effort into their top partners; increasing relationship quantity means that they increase the extent to which they spread their social effort among social partners (Box 1). As a result, the individual network in the top right is not simply a network with many strong relationships, but one with many relationships and a marked difference between the few strong relationships and the weaker ones.

The socio-ecological pressures and corresponding social solutions discussed here are not exhaustive, but illustrative examples meant to inspire further inquiry. For example, we have included infectious disease as a local pressure – something that comes about, in part, as a cost of socializing. But of course, disease exposure, avoidance, infection, and recovery can all intersect with social factors in myriad ways, dependent in part on the pathogen, its transmission pathways, virulence levels, and responsiveness of the immune system to it [76, 129-131]. The complexity of disease ecology warrants an entire framework with respect to the function of social relationships unto itself and has received only superficial treatment here.

Finally, there are other important factors, such as kinship, life history, and demographic patterns, that we have not addressed but that interact with socio-ecological pressures to shape the required and realized functions of social relationships and structures. We refer to excellent reviews on how these factors impact social relationships [132-138]. By approaching the study of social relationships from multiple angles, we can better untangle the complexity of the forces driving their variation [139]. Each perspective offers a unique piece of the puzzle, and ultimately, bringing these different pieces together will be essential for gaining a more complete understanding of the evolution of societies.

5. Concluding remarks and future perspectives

Social relationships appear to have adaptive value across a wide range of taxa, but exactly why that is the case remains unclear. To fill this gap, we propose the Adaptive Relationships Framework, unifying classic socio-ecological theory with fundamental ideas from network science about different types of social relationships and their functions. Testing this framework will require systematic studies across taxa and environments (Box 2). These studies should not only quantify the fitness benefits of social relationships, but also compare the relative importance of relationship quality and quantity, and test why each dimension of sociality is adaptive by linking it to the social solutions those relationships provide. This approach will clarify two fundamental outstanding questions: (1) which types of social relationships are adaptive, and (2) which pathways link social relationships to fitness in a given socio-ecological context. With the Adaptive Relationships Framework, we provide predictions that are broad enough both conceptually and operationally to be tested across a variety of taxa [Box 2; 140]. Fully realising its potential will require expanding research beyond well-studied systems, measuring social relationships in ways that lend themselves to comparative approaches, and investigating the generative processes that underlie social relationships and networks (see Outstanding questions). Ultimately, this will generate broad insights into the factors that shape social relationships and societies across the animal world, and will reveal the reasons why social relationships evolved.

Glossary

Relationship quality: The strength and stability of an individual's relationships relative to their other relationships. An individual who prioritizes relationship quality invests most of its social effort into strong, enduring relationships with a few partners.

Relationship quantity: The number of relationships an individual has and how well it is integrated into its wider social network. An individual who prioritizes relationship quantity spreads its social effort across many partners.

Social cohesion: The extent to which all individuals in a network are connected, regardless of the strength of their relationships. A cohesive network is one where most individuals are connected to each other.

Social differentiation: The extent to which the strength of relationships in a network varies. A differentiated network is one where some relationships are very strong, while others are weak or non-existent.

Social effort: The total amount of time and energy individuals invest in developing and maintaining their social relationships.

Social network: A representation and quantification of the social structure of a social unit [141].

Social organization: The size and composition of a social unit, including the sex, age and kinship relationships of its members [1].

Social relationship: The content, quality, and patterning of repeated interactions between two individuals [3]. In this paper, we refer specifically to affiliative social relationships, which emerge from repeated positive interactions.

Social structure: The content, quality, and patterning of social relationships among members of a social unit [3]. In this paper, we refer specifically to the social structure of affiliative social relationships.

Social support: Receiving active help, resource sharing, or care from social partners, which offers protection in risky situations and access to valuable resources. Providing social support comes at high cost and risk and requires mutual trust between partners.

Social tolerance: Being allowed to remain in close proximity of social partners without receiving aggression, leading to higher social integration and centrality. Granting social tolerance involves little cost or risk and is often mutually beneficial.

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