The importance of individual-to-society feedbacks in animal ecology and evolution

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Abstract

1. The social decisions that individuals make—who to interact with and how frequently—gives rise to social structure. The resulting social structure then determines how individuals interact with their surroundings—resources and risks, pathogens and predators, competitors and cooperators.
2. However, despite intensive research on (i) how individuals make social decisions and (ii) how social structure shapes social processes (e.g. cooperation, competition and conflict), there are still few studies linking these two perspectives. These perspectives represent two halves of a feedback loop: individual behaviour scales up to define the social environment, and this environment, in turn, feeds back by shaping the selective agents that drive individual behaviour.
3. We first review well-established research areas that have captured both elements of this feedback loop—host-pathogen dynamics and cultural transmission. We then highlight areas where social structure is well studied but the two perspectives remain largely disconnected. Finally, we synthesise existing research on 14 distinct research topics to identify new prospects where the interplay between social structure and social processes are likely to be important but remain largely unexplored.
4. Our review shows that the inherent links between individuals' traits, their social decisions, social structure, and social evolution, warrant more consideration. By mapping the existing and missing connections among many research areas, our review

highlights where explicitly considering social structure and the individual-to-society feedbacks can reveal new dimensions to old questions in ecology and evolution.

Keywords. Fitness, individual differences, group-living, social evolution, social networks, social structure, social transmission, coevolution, social dynamics

1. Introduction

Social interactions are a crucial component of animals' environments. As animals move and interact with others, they generate an ever-changing social web. Within this web, each individual experiences a unique social environment, and contributes to the social environment of others. The characteristics of the individuals' social environment can have profound implications for their reproduction and survival (e.g. Alberts 2019, and references therein). For example, an individual's mating opportunities or risk of contracting a disease, depend on its connections to other individuals. Explicitly accounting for the patterns of connections that form individuals' social environment—how connections are formed, maintained, and their short- and long-term consequences—represents a foundational shift in biological thinking in ecology and evolution (Wilson 1975; Kurvers *et al.* 2014). Such thinking represents a move away from models and assumptions that all individuals are connected (or connected equally) with one-another. However, this accounting has traditionally been done by asking questions from one of two perspectives: (i) how do individual traits influence their position in their social environment?, and (ii) how does population structure shape social processes, such as cooperation, competition, conflicts, and risks? Yet, these two perspectives are not independent. Individual behaviour scales up to define the social structure of the population; the resulting social structure, in turn, feeds back onto individuals' lives by modulating processes that can shape their fitness. Thus, these two perspectives represent two halves of a feedback loop (Fig. 1a).

Studies over the past decades have substantially advanced our understanding of the mechanisms by which social structure—the content, quality, and patterning of social connections among individuals in a population (Hinde 1976)—arises, and how social structure shapes social processes (Sueur *et al.* 2019). For example, (dis)assortativity around individual traits and states—e.g. genetic relatedness, sex, age, dominance, promiscuity, behavioural repertoire—can influence social interactions (Pike *et al.* 2008; Croft *et al.* 2009; Farine, Montiglio & Spiegel 2015; McDonald *et al.* 2019); early-life conditions affect adult social decisions (Farine, Spencer & Boogert 2015); and the social environment can affect collective decision-making (Strandburg-Peshkin *et al.* 2017; Palacios-Romo, Castellanos & Ramos-Fernandez 2019) or dispersal and recruitment (McDonald 2007; Ilany *et al.* 2013; Armansin *et al.* 2020). Sometimes, who individuals are connected to, or the overall structure of populations, can also simply arise from limitations in where individuals can move and, therefore, who they can encounter (e.g. He, Maldonado-Chaparro & Farine 2019). There is also an increasing understanding of how social structure shapes social processes. Different characteristics of social structure, such as the density of connections among individuals or their tendency to form interconnected clusters, can alter the breadth and diversity of behavioural repertoires (Cantor & Whitehead 2013; Aplin 2016), influence the resilience of a population against disturbances (Formica *et al.* 2017; Lantz & Karubian 2017; Maldonado-Chaparro *et al.* 2018a), and shape social processes such as competition (Sheppard *et al.* 2018) and the transmission of diseases and information (Aplin *et al.* 2012b; Stroeymeyt *et al.* 2018). Hence, structure and process are inherently linked.

Social structure represents a major substrate for evolutionary dynamics. It influences how selection, arising from either physical or biotic interactions, operates on phenotypes, including both social and non-social traits (Formica *et al.* 2011; Farine & Sheldon 2015; Sueur *et al.* 2019). Social structure, in and of itself, can also determine how individuals respond to selection (Montiglio, McGlothlin & Farine 2018), revealing the potential for co-evolution between the structure of the social environment and social processes. Ultimately, co-evolutionary pathways exist because both individuals and their social structures are coupled and dynamic systems (Box 1): individual social decisions underpin the social structures that, in turn, influences their behaviour. Despite the broad understanding of the many factors affecting the emergence and consequences of social structure, there are still few areas of research that explicitly capture the feedback between individual animals and their social structures. We generally refer to the factors that represent the two sides of the feedback as bottom-up and top-down effects, as they correspond to individuals' actions shaping social structure (bottom-up) and to processes that affect the environment that individuals experience (top-down).

Here, we highlight current efforts and recent opportunities for studying the individual-to-society feedback. We first review two well-established topics that have captured the feedback between individual behaviour and population-level processes: host-pathogen dynamics and cultural transmission (Fig. 1b). We then highlight how multiple mechanisms and population processes that have typically been explored separately could couple to form largely unexplored feedbacks. Finally, we synthesise the literature on social structure from the past decade to identify new prospects—research topics where evidence suggests that feedbacks between individuals and social structures are important, but where social structure has not been strongly considered. This synthesis provides a roadmap for strengthening existing, and arising, links between currently disparate research topics (Fig. 2, Box 1), which we believe will help to uncover new perspectives in the study of social evolutionary ecology.

2. **From individuals to societies and back: two established feedback loops**

Two well-studied dynamics in animal societies are the spread of infectious diseases and resulting host-pathogen evolution, and the spread of information and resulting cultural evolution. In both these examples, individual state (e.g. infected or not, informed or not) and processes (disease and information transmission) that operate through social structure are dynamic and tightly coupled (Fig. 1b), changing each other over time.

2.1. Infectious disease and parasite transmission

Social structure can fundamentally determine the pathways and consequences of pathogen transmission (Silk *et al.* 2019). Evidence for this comes from studies showing that the basic reproductive number (R_0), which is defined as the mean number of secondary infections in a susceptible population resulting from contact with a single infected individual during its infectious period (Macdonald 1952), typically misestimates the resulting rate of pathogen spread in structured populations (Keeling 1999). Thus, the patterns of contacts among individuals can generate differences in the propagation rate among populations, even with the same pathogen. For example, propagation is locally higher but globally lower when individuals' contacts are more clustered (Keeling 2005). The effects of social structure on disease propagation are evident when looking at how disease dynamics differ across taxa with varying social systems. Species where individuals have strongly-differentiated relationships are more susceptible to long-lasting outbreaks of low-transmissibility infections (Sah, Mann & Bansal 2018). Social connections can also provide a stronger medium for the transmission of some pathogens than alternative routes. For example, among giraffes (*Giraffa camelopardalis*), pathogen transmission is more likely to occur among socially-connected than spatially-connected individuals sharing a water-hole (VanderWaal *et al.* 2014). For endo- and ecto-parasites, the transmission process may not be restricted to direct contacts, but can also occur through indirect connections, such as shared space use (Silk *et al.* 2019). For example, the transmission of gastrointestinal helminths among Eastern chipmunks (*Tamias striatus*) can be temporally decoupled, by one or two weeks, from social contacts due to the life-cycle of the parasite (Grear, Luong & Hudson 2013). Together, these studies demonstrate that the pattern of the social structure and the nature of the pathogen or parasite interact to determine the transmission pathways and dynamics of disease spread. More recently, a similar feedback has been proposed regarding the dispersal of mutualistic and commensal microorganisms through social contact—while the microbial transmission can be modulated by the hosts' social environment, the hosts' physiology can in turn modulate the microbiota of that social environment (see Sarkar *et al.* 2020).

Social structure can shape the pathways of pathogen transmission and thus, can act as an agent of selection on the traits such as virulence and infectiousness, in both hosts and pathogens. Host resistance and pathogen virulence are textbook examples of co-evolutionary forces—increasingly virulent pathogens select for more resistant hosts. However, sociality presents an alternative medium through which host organisms can respond to pathogen virulence. Changes in host behaviour, such as to avoid pathogens (e.g. Prado *et al.* 2009), can drive selection on pathogen traits. For example, by reducing the ability for pathogens to spread, clustering of social interactions can select for lower pathogen infectivity (Boots & Mealor 2007), lower pathogen virulence (Best *et al.* 2011), and longer infection periods (Best *et al.* 2011). In turn, the impact of increased clustering of social interactions on pathogen traits can then drive the evolution of higher host resistance (Best *et al.* 2011); (Kiesecker *et al.* 1999; Behringer, Butler & Shields 2006; Boillat *et al.* 2015). These examples highlight how the patterns of connections that form social structure (e.g. clustered vs. unclustered), and not just the intensity of social behaviours (e.g. the number of connections), can directly shape key parameters of infectious diseases transmission dynamics.

Evolutionary changes in host or pathogen states could feed back onto social structure. Theory suggests that the relationship between pathogen prevalence, virulence, and host sociality is complex and, sometimes, counter-intuitive (Prado *et al.* 2009). In general, increasing pathogen prevalence can drive decreases, either evolutionary or behavioural (e.g. Prado *et al.* 2009; Stroeymeyt *et al.* 2018) in host-host contact rates, as individuals could be selected to avoid sick conspecifics (Kiesecker *et al.* 1999; Behringer, Butler & Shields 2006; Boillat *et al.* 2015) and sick individuals may even altruistically avoid kin (Heinze & Walter 2010; Bos *et al.* 2012; Stroeymeyt *et al.* 2018). However, a pathogen that is sufficiently contagious as to be unavoidable can drive an increase in host-host contact rates (Bonds *et al.* 2005), because the benefits of avoiding social contacts are lost while the benefits of maintaining contacts are maintained. Such co-evolutionary dynamics between host and pathogen parameters are potentially cyclical (Prado *et al.* 2009). High host sociality facilitates rapid transmission of pathogens and evolution of higher virulence, which, in turn, may drive a reduction in host sociality. As hosts evolve to have fewer contacts, selection on pathogens can favour reduced virulence (if hosts die before the pathogens can transmit). As virulence drops, host sociality increases, and the cycle continues. These examples highlight some of the ways in which the social structure of the population is important for cycling dynamics, and is also itself potentially dynamic.

From the perspective of studying animal social behaviour, one hypothesis for the evolution of social structure suggests that host-pathogen dynamics have driven the choice of social contacts (Freeland 1976). Specifically, can pathogens change the dynamics of social interactions within a group by selecting for social connections based on specific health traits of potential associates, thus leading to a clustered structure driven by the host-pathogen dynamics? If pathogens manipulate host behaviour to their benefit (Poulin 2018), or hosts respond to pathogens, such as by reducing social contacts when infected (Lopes, Block & Konig 2016), then host-parasite interactions could impact social structure dynamically. Black ants (*Lasius niger*), for example, if challenged with a pathogenic fungus, individual-level changes in the patterns of social contacts increase transmission-inhibiting structural properties at the colony-level (Adelman *et al.* 2015). However, individuals are not homogeneous; they can also vary in their infectiousness, in their contact rates, and in their infectious period (VanderWaal, Ezenwa & Hawley 2016). Thus, we could ask whether and how heterogeneity among individuals, or in their social relationships, affect co-evolutionary dynamics between hosts and pathogens. For example, common vampire bats (*Desmodus rotundus*) expressing sickness behaviour reduce their social interactions (such as allogrooming with non-kin), but these reductions are smaller for social interactions that generate greater benefits (such as food sharing with close kin) (Stockmaier *et al.* 2020). Some individuals contribute disproportionately to propagations of pathogens, such as when 20% of individuals contribute 80% of the transmission events (Lloyd-Smith *et al.* 2005; Adelman *et al.* 2015). If infectiousness and contact rates can be modulated through social behaviour, which can be either host-driven (e.g. to avoid infection) or pathogen-driven (e.g. manipulating host behaviour), and infectiousness and contact rates co-vary, then both the social structure and disease parameters (e.g. virulence) should be dynamic in a given population.

2.2. *Information and cultural transmission*

Although fundamentally different, information and pathogens can sometimes spread through populations in similar ways. Animals often use information from their social contacts when making decisions about foraging, habitat choice, and predator avoidance (e.g. Doligez, Danchin & Clobert 2002; Gil *et al.* 2018). However, since individuals rarely have access to all other individuals in their population, social structure constrains where and when information can spread (e.g. Aplin *et al.* 2012a), similar to social constraints on pathogen spread. Information transmission can also fundamentally differ from pathogen spread. For instance, transmission does not always follow a one-contact to one-spread rule ('simple contagion'), but can require more than one contact and social reinforcement via multiple interaction partners ('complex contagion') (Centola *et al.* 2007; Firth 2020). Complex contagion processes fundamentally alter the properties of transmission through populations, especially in those where social interactions are concentrated around a few individuals, or when individuals are somewhat segregated into distinct social clusters (Centola *et al.* 2007). In simple contagion processes, clusters of highly interconnected individuals impair transmission, but during complex contagion, clustering of individuals can instead facilitate transmission, as found in startle responses in schools of golden shiners (*Notemigonus crysoleucas*) (Rosenthal *et al.* 2015).

One property of information transmission, making it distinct from disease transmission, is that individuals can make decisions about producing or using information. Such decisions can alter transmission pathways and outcomes. For example, songbirds consider their social environment when producing vocal information to recruit new members to a foraging site (Suzuki & Kutsukake 2017; Hilleman *et al.* 2019) and chimpanzees (*Pan troglodytes*) adjust food-associated vocalisations depending on the strength of the social bond they have with the intended receiver (Slocombe *et al.* 2010). When individuals are faced with multiple sources of information, how they decide what to learn or who to learn from can also impact the information landscape (Kendal *et al.* 2018). Individuals may have different social learning strategies and preferentially copy individuals that are more dominant, successful, or older (Laland 2004; Kendal *et al.* 2015), thus shaping what information persists in a population. If individuals bias their learning towards a more common behaviour, then one variant can become entrenched in a population (Aplin 2016). For example, conformist transmission among great tits (*Parus major*) can lead to stable socially-learned foraging behaviours that are maintained across multiple generations (Aplin *et al.* 2015). However, the propensity for local traditions to become established and be maintained can also largely be determined by the global structure of the population, even when learning is conformist (Somveille *et al.* 2018). More clustered and modular social structures can promote local traditions. For example, orcas (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) live in multilevel societies with stable social groups and show group-specific repertoires of acoustic, foraging and social behaviours that are maintained over generations (Whitehead & Rendell 2014). Thus, the structure of populations as well as learning rules will determine what information is available to transmit and where it spreads, shaping the information landscape that individuals have available to them in their social environment.

When behaviours are socially-learned, shared within subgroups of the population, and persist over time, they are recognized as culture (Laland & Hoppitt 2003). Considering how learned behaviours can affect individual social decisions reveals the potential for culture to underpin the co-evolution between social structure and behaviour. For example, information state can determine the propensity for two individuals to associate, through a process called behavioural homophily (Centola *et al.* 2007; Cantor & Whitehead 2013). Information state can also determine the maintenance of social bonds—having similar social traits can facilitate cohesion among individuals by allowing them to synchronise and coordinate their activities (Coussi-Korbel & Fragaszy 1995). For example, populations of bottlenose dolphins are often divided into social communities assorted by learnt foraging tactics (Mann *et al.* 2012; Machado *et al.* 2019; Wild *et al.* 2019), illustrating the idea that the more individuals interact, the more opportunities they have for copying each other, thus highlighting how social decisions can reinforce behavioural homogeny. Models have shown that the feedback between information transmission and social decision-making can stimulate the formation of stable groups within otherwise unstructured, well-mixed, populations with (Cantor *et al.* 2015) and without any complex decision-making (Cantor & Farine 2018). Information state can also impact individual position within their social environment. More knowledgeable individual lemurs (*Lemur catta*) become more connected in their social environment (Kulahci, Ghazanfar & Rubenstein 2018); becoming more connected can then promote information transmission (Kulahci & Quinn 2019). Thus, there is extensive empirical and theoretical evidence for the feedback between information use and social structure.

Beyond determining which individuals acquire information, social structure can also play a role in shaping the quality and quantity of information, akin to pathogen virulence. Learning of new behaviours can be error-prone, thus social structures that result in longer transmission pathways (e.g. where information must take more steps to reach every individual in a population) should not only slow information transmission but also mean that individuals may acquire different, or lower quality information (reviewed in Cantor & Whitehead 2013). The propensity for learning errors to accumulate in longer transmission chains can subsequently promote diversity of information in populations (Whitehead & Lusseau 2012), with obvious consequences on variation in behavioural repertoires within populations arising from the correlation between connectedness in the social network and individual information state.

3. Multiple bottom-up and top-down influences in individual-to-society feedbacks

There are a multitude of social drivers and population processes that, unlike the topics above, are rarely considered in unison. We first synthesise how the state of individuals—including the conditions experienced in early-life, average genetic relatedness to conspecifics, and social dominance—can influence their social decisions and through these the emergent structure of their societies. Next, we synthesise how the emergent social structure influences processes such as population dynamics, social stability, and social selection, can translate to fitness outcomes and drive evolutionary dynamics.

3.1. Bottom-up: individual states influencing social structure

Social traits can be determined at young age. Early-life conditions can modulate later-life social behaviour, shaping the population-level social patterns along the way. For instance, zebra finch nestlings exposed to stress develop more gregarious social phenotypes, maintaining a greater number of social partners but choosing partners more randomly (Boogert, Farine & Spencer 2014; Brandl *et al.* 2019a). The proximate mechanisms that underpin inter-individual differences in the development of social behaviour are also becoming clearer. Early-life stress can influence the expression and receptor-binding of the neuropeptides oxytocin and vasopressin (Veenema 2012), which are important for the expression of social behaviours. Zebra finches with experimentally reduced vasotocin production are less gregarious (Kelly *et al.* 2011) and more aggressive (Kelly & Goodson 2014). These changes in phenotype can alter the individual's social environment with consequences on their later fitness.

A pillar of the social environment is the formation of preferred associations. Such social preferences are evident from partner investments that require time and energy (e.g. allogrooming) and consistent associations that cannot be explained by spatial ranging alone (e.g. mutual attraction to resources). For example, chimpanzees associate preferentially with individuals that reciprocate grooming (Mitani 2006), vampire bats that groomed and shared food in captivity stay together when released back to the wild (Ripperger *et al.* 2019), and zebra finches that bred synchronously in the same colony also foraged together outside of the breeding period (Brandl *et al.* 2019b). It remains unclear to what extent such preferred associations depend on prior experiences *versus* phenotypic traits. Individuals can have preferences for conspecifics with traits that either match or differ from their own. Such phenotypic assortment (Farine 2014) is a key driver of population-level social patterns (e.g. Croft *et al.* 2009; Apicella *et al.* 2012; Carter *et al.* 2015) and central to social evolution (Centola *et* *al.* 2007; McDonald *et al.* 2017). In some cases, associations themselves can drive phenotypic similarity as in vocal convergence in the contact calls of unrelated female greater spear-nosed bats (*Phyllostomus hastatus*) that form a group (Boughman 1998). However, the mechanisms by which new preferred associations form, are maintained, and develop into higher-value social relationships, is an important area for future research (Carter *et al.* 2020).

Kinship is perhaps the most well-known driver of social preferences. Kin-biased associations can result from either prior association or phenotype matching, which allows identification of unfamiliar kin (e.g. Holmes & Sherman 1982; Halpin 1991; Sharp *et al.* 2005). Although kin-biased associations provide opportunities for increasing inclusive fitness through nepotism, the benefits can be partially or completely negated by increases in the potential for inbreeding and kin competition (Keller 2002; West, Pen & Griffin 2002). The costs of inbreeding and kin competition vary with differences in dispersal and the spatial scale of competition. Therefore, some species, such as Australian sleepy lizards (*Tiliqua rugosa*), show kin avoidance (Godfrey *et al.* 2014), while others, such as sperm whales (*Physeter macrocephalus*), preferentially associate with kin (Konrad *et al.* 2018). Kin-biased assortment or dispersal (e.g. budding dispersal) (Gardner & West 2006) influences genetic structure and the potential for kin selection, with major consequences for the evolution and maintenance of cooperative behaviours (Hatchwell 2009; Green & Hatchwell 2018).

The structure of social relationships can also be moulded by many other factors, including agonistic interactions, phenotypic composition, and competition for resources. Rank within the dominance hierarchy can be determined by individual traits (Drews 1993), such as size, age or sex, or by social state, such as winner-loser effects (Chase *et al.* 2002) and social alliances (Strauss

& Holekamp 2019). Aggression can lead to dominance-related spatial structure, where group members position themselves closer or farther from each other depending on difference in rank (Hemelrijk 2000). Agonistic interactions with other groups can also shape within-group social structure. For example, the structure of lekking wire-tailed manakin (*Pipra filicauda*) populations was less stable when more high-testosterone individuals were present (Dakin *et al.* in press). When individuals compete for resources, the distribution and abundance of resources can impact individuals' decisions to form groups and whether to associated with preferred associates versus less preferred associates. For example, African lions (*Panthera leo*) associate more equally within a pride when prey are larger and aggregated, but associate more exclusively when prey are smaller or dispersed (Mbizah *et al.* in press).

3.2. Top-down: social structures influencing individual states

Social structure can influence social and larger-scale demographic and ecological processes, such as social stability (the pattern of recurrent relationships among group members), resilience (how a group responds and adjusts to external disturbances), and population dynamics, and these can shape the state of individuals and drive selection. Demographic processes (birth, death, emigration, immigration) can impact social stability (e.g. Beisner *et al.* 2011; Maldonado-Chaparro *et al.* 2018a; Shizuka & Johnson 2020), and determine the ability for individuals to express certain traits. For example, temporary splits in captive zebra finch colony membership disrupted the social relationships among colony members; in turn, these changes in social structure negatively affected foraging behaviour (Maldonado-Chaparro *et al.* 2018a). The same structural properties of disturbed social networks in the zebra finches were also found to be present in communities of Masai giraffes (*Giraffa camelopardalis tippelskirchi*) that overlapped with human settlements (Bond *et al.* in press). Even the loss of a single key individual can destabilize social structure (Flack *et al.* 2006) and alter patterns of mating or parental care (Silk 2007; Alberts 2019). Thus, there is extensive scope for demographic processes and social instability to shape individual-level states.

Social structure can affect broader population dynamics by influencing individual survival (Singleton & Hay 1983; Cameron, Setsaas & Linklater 2009) and life history traits, such as reproductive investment (Singleton & Hay 1983; Cameron, Setsaas & Linklater 2009). In alpine marmots (*Marmota marmota*), the number of helpers in the hibernaculum is positively correlated with over-winter survival (Grimm *et al.* 2003), and changes in the group size of meerkats (*Suricata suricatta*) determines the dynamics of female dispersal and birth rates (Bateman *et al.* 2013). A measure of direct and indirect early-life social connectivity (eigenvector centrality) also predicts adult survival in male bottlenose dolphins (*Tursiops* sp.) (Stanton & Mann 2012). Considering sociality beyond group size, composition, and density of social connections raises new questions such as: Do individuals contribute differently to population growth based on how well connected they are? Can phenotypic assortment shift the operational sex-ratio and thus the reproductive output of a population? Which mechanisms give rise to variation in social traits and how consistent are these traits over the course of an individual's lifetime? Identifying the social trait that best influence demographic processes is, in itself, an interesting question (Pelletier *et al.* 2007).

Social structure can influence how sexual and social selection are operationalised (McDonald *et al.* 2017; McDonald & Pizzari 2018b) and thus shape evolutionary processes by creating variation among individuals in their relative fit to their environment. For instance, male house finches (*Carpodacus mexicanus*) with less elaborate plumage can increase their relative attractiveness by moving more often between groups (Oh & Badyaev 2010). Dispersing great tits (*Parus major*) that arrive late to the breeding grounds are less likely to acquire a territory, unless they associate with other late arriving individuals (Farine & Sheldon 2015). Early-life connectivity can also dictate the acquisition of sexual traits that are expressed as adults. For example, juvenile male zebra finches acquire the song of their most strongly-associated adult male (i.e. the song that juvenile males learn) (Boogert *et al.* 2018). Being more socially connected as a juvenile predicts social rise to reproductive positions in long-tailed manakin males (*Chiroxiphia linearis*) (McDonald 2007) and increase longevity and reproductive success later in life in spotted hyenas (*Crocuta crocuta*) (Turner *et al.* in press). Thus, social structure across different time scales can impact the acquisition and value of individual traits, and social behaviour provides the scope for individuals to develop strategies that increase their chances of reproduction if they are physically outcompeted. Studies of social networks in hybrid populations provide opportunities to better understand the direct feedbacks between individual social traits, fitness outcomes, and population-level consequences. For example, Zonana *et al.* (2019) found strong links between social associations and mating outcomes in a hybrid population of California (*Callipepla californica*) and Gambel's (*Callipepla gambelii*) quail, even in the absence of structure in terms of genetic ancestry, suggesting an important role of social relationships in maintaining genetic structure in the population.

Explicitly quantifying individual-to-society feedbacks can reveal the relative importance of different levels of selection (Fisher & McAdam 2017), and their ecological or mechanistic bases (Pruitt *et al.* 2018). For example, if the consequences of social interactions are mediated by a genetic component in the individuals, the social interactions can provide an additional source of heritable genetic variance (Agrawal, Brodie & Wade 2001). In such cases, population structure can generate emergent variation in the social environment that each individual experiences, which is correlated among connected individuals (i.e. assortment), thus generating 'between-group' differences on which selection can act (Montiglio, McGlothlin & Farine 2018). Social phenotypes that are selected for via social or sexual selection can therefore feed back onto the social structure via distinct pathways. Many potential pathways exist, providing promising avenues for future research on individual-to-society feedbacks.

4. Future prospects for studying individual-to-society feedbacks

The importance of the links between individuals' traits, their social decisions, social structure, and social evolution are likely to be much more prevalent than currently considered. The concepts of bottom-up and top-down social influences are newly emerging across several research fields, revealing rich opportunities for new research questions (Sueur *et al.* 2019; Shizuka & Johnson 2020). Here we synthesise key research topics where individual-to-society feedbacks are important yet remain underexplored.

4.1. Social inheritance

Theory suggests that social structure can emerge and be maintained across generations by a simple mechanism of offspring having a higher probability of establishing relationships with their parents' associates (Ilany & Akcay 2016b; Ilany & Akcay 2016a). This mechanism can help explain social clustering and heterogeneity of social interactions across a range of taxa. The process by which offspring inherit social traits from their parents via the social environment is called social inheritance (Ilany & Akcay 2016b).

Social inheritance can underpin the transgenerational transmission of social roles and other behaviours (Ilany & Akcay 2016b; Cantor & Farine 2018). For example, African elephants (*Loxodonta africana*) live in multi-level (i.e. structured in hierarchically nested social levels of organization), matrifocal (i.e. structured around a female), societies where the relationships between the maturing young and the matriarch provide calves with opportunities to replicate the matriarch's social environment (Goldenberg, Douglas-Hamilton & Wittemyer 2016). Similarly, in spotted hyenas, the amount of social support, rather than intrinsic attributes (e.g. physical strength and aggressiveness), explains the outcome of one-on-one interactions in the process of establishing dominance, and thus offspring social rank (Strauss & Holekamp 2019; Vullioud *et al.* 2019). In theory, social inheritance can also facilitate phenotypic assortativity by causing individuals to be more connected with kin or otherwise similar groupmates. For example, populations can become assorted by personality if both personality and social contacts are heritable (Ilany & Akcay 2016a). Despite its explanatory power, social inheritance, and other mechanisms such as genetic inheritance of behavioural traits, remains an underexplored bottom-up driver of real animal societies and the evolution of other social interactions, such as dominance interactions (but see Strauss, Shizuka & Holekamp 2019). Further, little is known about the top-down consequences of inheriting social contacts in other aspects of an individual animal's life, such as survival and lifetime reproductive success.

4.2. *Predator-prey dynamics*

Predation risk plays a major role in group living, and there is increasing evidence that it shapes social structure. Individual predation events cause flocks of great tits (*Parus major*) to rapidly reconfigure (Voelkl, Firth & Sheldon 2016), while long-term predation pressure promotes more stable schools in Trinidadian guppies (*Poecilia reticulata*) (Heathcote *et al.* 2017) and drives more complex social interactions in cooperatively-breeding cichlids (*Neolamprologus pulcher*) (Groenewoud *et al.* 2016). There is also a growing body of work showing how social interactions between predators can drive the evolution of prey traits. Studies of great tits as predators illustrate how social interactions—specifically social learning—can reinforce the evolution of prey defences, such as aposematic warning signals (Landova *et al.* 2017; Thorogood, Kokko & Mappes 2018).

However, how the social structure of predators can feed back on the prey's, and vice-versa, has yet to be explored in detail. If social relationships in either predator or prey populations exhibit phenotypic structure (e.g. assortment by predator or anti-predator traits), then this could alter the 'landscape of fear' by generating non-random social or spatial structure in susceptibility to predation (Gotanda *et al.* 2019). In turn, social structure could shape the strength and direction of selection for different individuals (Pruitt *et al.* 2017). For example, if predators overlap with multiple prey groups, then the traits of one prey group can affect the predator's behaviour (e.g. whether it becomes satiated or not), which can, correspondingly, create an indirect effect on the predation pressure that another prey group experiences (e.g. whether it is attacked or not) (Montiglio *et al.* 2018). The interplay of social structures within and across trophic levels, and across meta-populations, remains a rich area for future research, with co-evolutionary dynamics arising from social structure potentially taking place between predators and prey, and within both predator and prey communities.

4.3. Collective decision-making

Theory suggests that animals moving together cant maintain cohesion and coordinate behaviours by following simple rules such as attraction, repulsion and alignment to other group members (Couzin *et al.* 2002). In species that maintain preferred relationships, individual social preferences can determine closest neighbours (Farine *et al.* 2017), and thus the composition of a unit of interacting individuals. Simulations suggest that preferred associations can generate sub-group formation, and cause more socially-connected individuals to be closest to the group centre (Bode, Wood & Franks 2011). In this way, emergent group-level behaviours can directly affect fitness by driving local variation in how individuals experience their environment, such as their relative predation risk.

Not only can individuals' social preferences in collective movement influence social structure, but the structure itself can also impact collective movement and decision-making. Social relationships can determine the relative influence of each individual on their group (Strandburg-Peshkin *et al.* 2018). For example, individual chacma baboons (King *et al.* 2011) and Geoffroy's spider monkeys (*Ateles geoffroyi*) (Palacios-Romo, Castellanos & Ramos-Fernandez 2019) are more likely to be followed by close associates when initiating movement. If followership is explained by relatedness or affiliations to others, then individuals that are more socially connected can be more influential by being more effective at recruiting a majority (Strandburg-Peshkin *et al.* 2015). Collective actions, such as joint territory defence, can also feed back onto affiliative behaviours and fitness. For example, green woodhoopoes (*Phoeniculus purpureus*) increase allopreening rates (increasing the connectivity among group members) after coordinating their behaviours during inter-group conflicts (Radford 2008), whereas groups of banded mongoose (*Mungos mungo*) express lower within-group agonistic interactions after simulated intergroup conflicts (thereby reducing social connectivity within the group) (Preston *et al.* in press). A ripe direction for future research is to integrate the study of how social structure shapes the properties of animal collectives with the feedback that collective decision-making has on individual interaction rules and social structure.

4.4. Dispersal behaviour

Dispersal to, and subsequent reproduction in, newly-settled environments is the primary driver of gene flow and connectivity across populations (Bowler & Benton 2005). The outcomes of individual dispersal decisions can also generate social structure. In most species, the young of one sex disperse sufficiently far to reduce the chances of encountering related individuals (Clobert 2012). If there is limited dispersal (Hamilton 1964a), budding dispersal (Gardner & West 2006), or any pattern where dispersing individuals are more likely to encounter kin (Leedale *et al.* 2018), then kin-structured populations can emerge, which can be important for the evolution of cooperative breeding (Hatchwell 2009; Green & Hatchwell 2018).

Dispersal decisions fundamentally drive social structure, which has reciprocal consequences for individual dispersal decisions. Local density increases competition for resources, which can determine when individuals disperse and where they go (Maag *et al.* 2018). Aggressive (Christian 1970) and affiliative (Bekoff 1977) interactions can also underpin decisions to disperse or not. In yellow-bellied marmots (*Marmota flaviventris*), females that are more socially-embedded in their natal group are less likely to disperse (Blumstein, Wey & Tang 2009). Social interactions can also influence patterns of settlement. In songbirds, associations during the winter predict breeding and territorial proximity in the following spring (Firth & Sheldon 2016). In group-living birds (Williams & Rabenold 2005) and primates (Cheney & Seyfarth 1983), individuals often disperse between neighbouring groups, highlighting a link between global social structure and dispersal decisions. Finally, social structure can determine how difficult new social environments are for dispersers to penetrate (Armansin *et al.* 2020). In rock hyraxes (*Procavia capensis*), some groups are more resistant to immigrants if the addition of a group member disrupts otherwise stable social associations (Ilany *et al.* 2013).

Studies of the transience stage of dispersal may provide opportunities to explore the feedback between animals' dispersal decisions and social structure. Transience represents a key point where individual decisions directly translate to social structure. During transience, dispersing coalitions of Kalahari meerkats (*Suricata suricatta*) avoid territories of unrelated groups (Cozzi *et al.* 2018) and disperse shorter distances when cohorts are larger and contain more males (Maag *et al.* 2018). Despite being a critical stage in the interplay between top-down and bottom-up processes, transience behaviours remain understudied, especially in social species (Mabry *et al.* 2015). A promising avenue for future work is quantifying the role of population-level social structure (i.e. the social landscape) in shaping the movement and prospecting behaviours of dispersers (e.g. Armansin *et al.* 2020) which can, in turn, alter patch-level social structure through settlement.

4.5. Cooperative behaviour

Cooperation involves providing benefits to social partners. How cooperation evolves and is maintained in animal populations has sparked debate on the relative merits of competing theoretical frameworks: inclusive fitness, multilevel selection, reciprocity, and biological markets (West, Griffin & Gardner 2007; Carter 2014). Although these theories differ, they all imply that the evolutionary stability of costly cooperation requires some form of spatial, phenotypic, or behavioural assortment (Hamilton 1964b) where individuals with a greater tendency to cooperate preferentially interact with each other to avoid the costs of defection by non-cooperators (Fletcher & Doebeli 2009; Apicella *et al.* 2012; Marcoux & Lusseau 2013).

Considering social structure is therefore essential for an ecologically realistic understanding of the evolution and maintenance of social cooperation. Cooperation can be favoured by repeated interactions (Axelrod & Hamilton 1981), caused by strong pairwise social ties (Allen *et al.* 2017), but disfavoured in populations with a high density of social connections as these are more easily invaded by non-cooperators (Ohtsuki *et al.* 2006). In addition, higher levels of cooperation can be maintained when individuals choose their associates—as cooperators prune their social ties with defectors—thereby affecting social structure by creating clusters of highly cooperative individuals (Fehl, van der Post & Semmann 2011). This process can occur through kin selection, but costly nonkin cooperation can also be maintained via conditional partner choice and partner control. By monitoring their experiences with others, individuals can choose more cooperative partners, reward cooperative behaviour, and punish defection (Agren, Davies & Foster 2019). For example, flycatcher pairs preferentially mobbed with neighbouring pairs that helped them mob previously (Krams *et al.* 2007; Krama *et al.* 2012), vervet monkeys received more grooming after their ability to provide food was experimentally elevated (Fruteau *et al.* 2009), and dwarf mongoose received more grooming after their perceived contributions to cooperative sentinel behaviour were experimentally elevated by playbacks (Kern & Radford 2018).

Some experimental evidence suggests that individuals that experience cooperation with one set of partners are more likely to cooperate with a different set of partners (generalized reciprocity) (e.g. Rutte & Taborsky 2007; Barta *et al.* 2011). In other words, when deciding to cooperate, individuals might not only monitor the cooperativeness of specific individuals but also their overall social environment. This possibility opens interesting new questions about individual-to-society feedbacks. While experiments suggest that the regularity of social interactions can promote cooperation in humans (Rand, Arbesman & Christakis 2011), would the social stability or quality of social relationships influence the cooperation strategies of individuals within non-human societies? For example, does a more stable social environment reward vampire bats with fewer stronger relationships, while unstable social environments favour bats with more but weaker social ties (Carter, Farine & Wilkinson 2017)? If an individual grows up in a more cooperative society, does that experience make it more likely to cooperate with new individuals in a different society?

4.6. Mating systems

Mating systems are influenced by two main factors, the spatiotemporal distribution of males and females, and the extent to which each sex invests in parental care (Emlen & Oring 1977). However, mating systems are also impacted by social structure since males and females do not interact homogenously, either within or between sexes. Heterogeneity in social interactions can result from intrinsic (e.g. homophily) or extrinsic (e.g. predation risk, habitat structure) factors, and can influence the spatial and temporal distribution of individuals, thus leading to individual variation in competitive environments and mate availabilities (McDonald *et al.* 2013; Maldonado-Chaparro *et al.* 2018b). Local differences in density and operational sex ratio (Kasumovic *et al.* 2008) or in the phenotypic composition of the social environment (Farine, Montiglio & Spiegel 2015) can generate fine-scale differences in the strength and direction of sexual selection on individual morphological or behavioural traits.

Individuals can also express differences in mating strategies (e.g. in promiscuity) and can respond to experienced selection pressures. For instance, males that mate with many females might also mate with the most polyandrous females (McDonald & Pizzari 2018a), or males might decide to leave a highly competitive area, which can feed back to social and mating structure (Watters & Sih 2005). For instance, in water striders the presence of aggressive individuals drives other individuals to leave the area shaping new local group compositions (Eldakar *et al.* 2009). In such a case a male's reproductive success will not only depend on his direct competitors, but also on females' connections to their potential mates. Thus, males who have the greatest copulation success also suffer from the highest intensity of sperm competition, thus generating post-copulatory sexual selection (Fisher, Rodriguez-Munoz & Tregenza 2016). The mating structure of animal populations represents a clear example of how social structure both acts to shape selection and how it can be shaped by individuals responding to competition for reproductive success.

4.7. Physiological interactions and stress transmission

Behavioural endocrinologists have long recognized a two-way relationship between physiology and behaviour. Even indirect social interactions can affect an individual's physiology. For example, observing agonistic interactions increases androgen levels of uninvolved cichlid fish (*Oreochromis mossambicus*) (Oliveira *et al.* 2001), and the heart beat rate of bystanders in greylag geese (*Anser anser*) (Wascher, Scheiber & Kotrschal 2008). Social position, including rank in the social hierarchy, can also impact stress levels and health (Sapolsky 2005). Just as social structure and interactions shape individuals' physiological states (comprising reproductive state, metabolic state, seasonal variation in hormone levels, and other aspects), these states can influence who individuals associate with, potentially driving assortment by physiological traits. Very simple processes can promote non-random clustering among individuals. For example, individuals sharing physiological traits might move at the same speed or have similar nutritional demands and therefore have a higher propensity for spatial and social clustering (Gersick & Rubenstein 2017). The divergent behavioural outcomes linked to the physiological phenotypes of individuals (re)shape their social environment. For example, if closely associated individuals are more (dis)similar in their physiological states, such (dis)assortativity could indicate another link between individual traits and processes mediated by social structure.

One physiological aspect with potential for an integrative study of feedbacks between individuals and societies is the stress response within the social environment. Activation of the neuroendocrine stress axis usually leads to an elevation of stress-associated glucocorticoids, which are known to play a role in various forms of social behaviour of vertebrates (Spencer 2017) and can shape how individuals interact with others (DeVries *et al.* 1996). Physiological expression of individual states, such as stress, might transmit to other individuals via social interactions (Noguera, Kim & Velando 2017). On the other hand, social support in the group can mitigate stress responses (Furtbauer & Heistermann 2016) and facilitate coping with stressful events (social buffering) (Kikusui, Winslow & Mori 2006). For instance, lactating chacma baboon females that are strongly connected to males have lower glucocorticoid levels when faced with newly immigrated, and potentially infanticidal, males (Engh *et al.* 2006). The absence of such social support (i.e. social isolation) can, in turn, have negative effects on fitness: in greylag geese, solitary confinement or mate-loss affects immuno-reactive corticosterone metabolites, percentage of red blood cells, and intestinal parasite loads (Ludwig *et al.* 2017).

Integrating the individual's state, the response of the group, and following it back to the individual might generate new insights on how social groups respond to environmental stressors. Observing individuals under environmental pressures that push their physiological limits, such as food or water shortages, high temperatures, or increased predation, can provide an opportunity to study feedbacks and behavioural drivers. Experimental approaches might involve changing the composition of physiological phenotypes in groups to test whether it changes the social structure. While traditional studies might have ended at this point, observing follow up changes in individual states, resulting from a shift in selective agents of the social environment, might generate new insights on feedback mechanisms. While the investigation of the link between physiology and the social environment is slowly emerging (Seebacher & Krause 2017), a thorough empirical framework for an integrative study of the feedback of physiological states remains an exciting and promising new avenue for research.

5. Closing remarks

Our synthesis captures the growing evidence that individual decisions leading to social structures can influence a wide range of social and ecological processes, and that these can, in turn, influence how individuals behave and interact further. Theoretical and empirical research on host-pathogen dynamics and cultural transmission clearly illustrates how social structure is at the centre of a feedback between the social decisions that individual animals make and social structure, and how social processes that are shaped by social structure can impact individual traits. However, the implications of such feedback loops for the ecology and evolution of animal societies are likely to go beyond these well-established areas of study, potentially affecting more processes than those considered here.

We highlight existing opportunities to integrate disparate areas of research (Fig. 2) into the study of individual-to-society feedback loops. Some topics (and their relationships to each other) are quite well explored, such as relatedness, cooperation, and information and cultural transmission. However, there are many gaps—for example how relatedness links to the stability and resilience of societies—with some linkages between topics having only been tentatively explored. Further, animal societies are likely to be simultaneously shaped by multiple factors. For example, relatedness could determine the susceptibility of individuals to the pathogens that their social contacts have, and therefore the parameters of pathogen transmission. Thus, most top-down processes could act in unison with other top-down processes, or represent a feedback to most bottom-up processes. Addressing such aims will be challenging, requiring a combination of tools, such as high-resolution tracking, experimental manipulations, study systems that are amenable to such manipulations, and analytical techniques that can clearly identify the process or effect of interest amongst the competing drivers.

Individuals and societies are both dynamic, adaptive systems. Yet, most of the research being conducted in animal societies focuses on either top-down or bottom-up approaches. Here, we suggest that an integrative approach that explicitly considers the feedback between current individual states and the social environments they experience will generate new insights on the ecology and evolution of animal social systems. In generalizing the individual-to-society feedbacks to include a more diverse array of bottom-up and top-down influences, we can gain a broader understanding of the dynamics of social systems and the evolution of animal societies.

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Authors’ contributions

DRF developed the concept and scope of the synthesis. MC, AMC, DRF defined the structure of the manuscript and led the writing. All authors contributed to writing and revising sections, overseen by DRF, MC, AMC. Authors are otherwise listed alphabetically.

Data accessibility

The search terms and the closely-related terms used to perform the bibliographical review, the list of publications gathered from Web of Knowledge, and the R code to replicate the network analysis are available in Supporting Information S1.

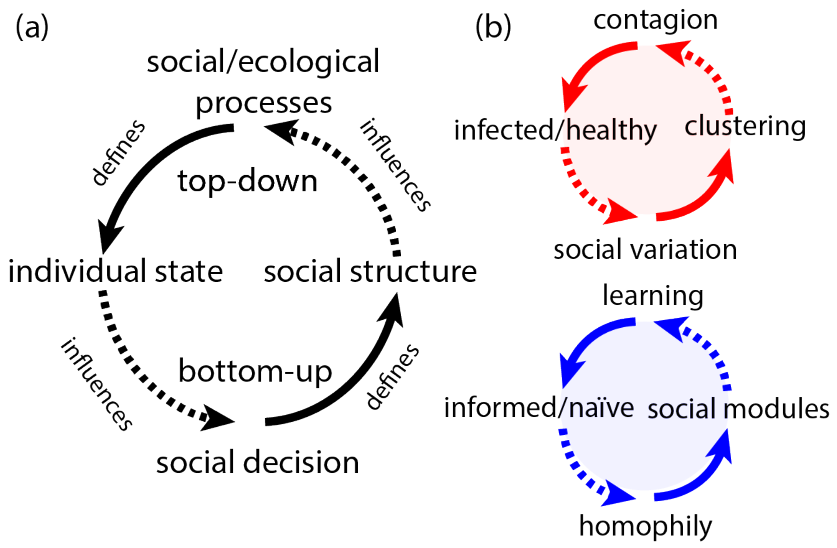

Figure 1. The individual-to-society feedback. (a) A generalized feedback loop between individual states and social structure considering that animals and their societies are linked. Bottom-up influences represent social decisions that contributes to the resulting social structure. Top-down influence are the effects of social structure (i.e. the distribution of social ties among individuals) on social and ecological processes that ultimately determine the state of the individuals. (b) Individual-to-society feedbacks illustrated for pathogen (top) and information transmission (bottom). Whether or not individuals are infected by a pathogen or parasite can influence the number of social connections they have, shaping social structure, which will define properties of spread in populations (including pathogen traits), and ultimately determine the future state of individuals (infected or healthy). Similarly, individuals that are informed or naïve to a behavioural tactic can have a higher tendency to interact among themselves (homophily), shaping the population into social modules; such modular structure will define how the tactic will spread in the population via learning and ultimately define the future state of individuals (informed or naïve).

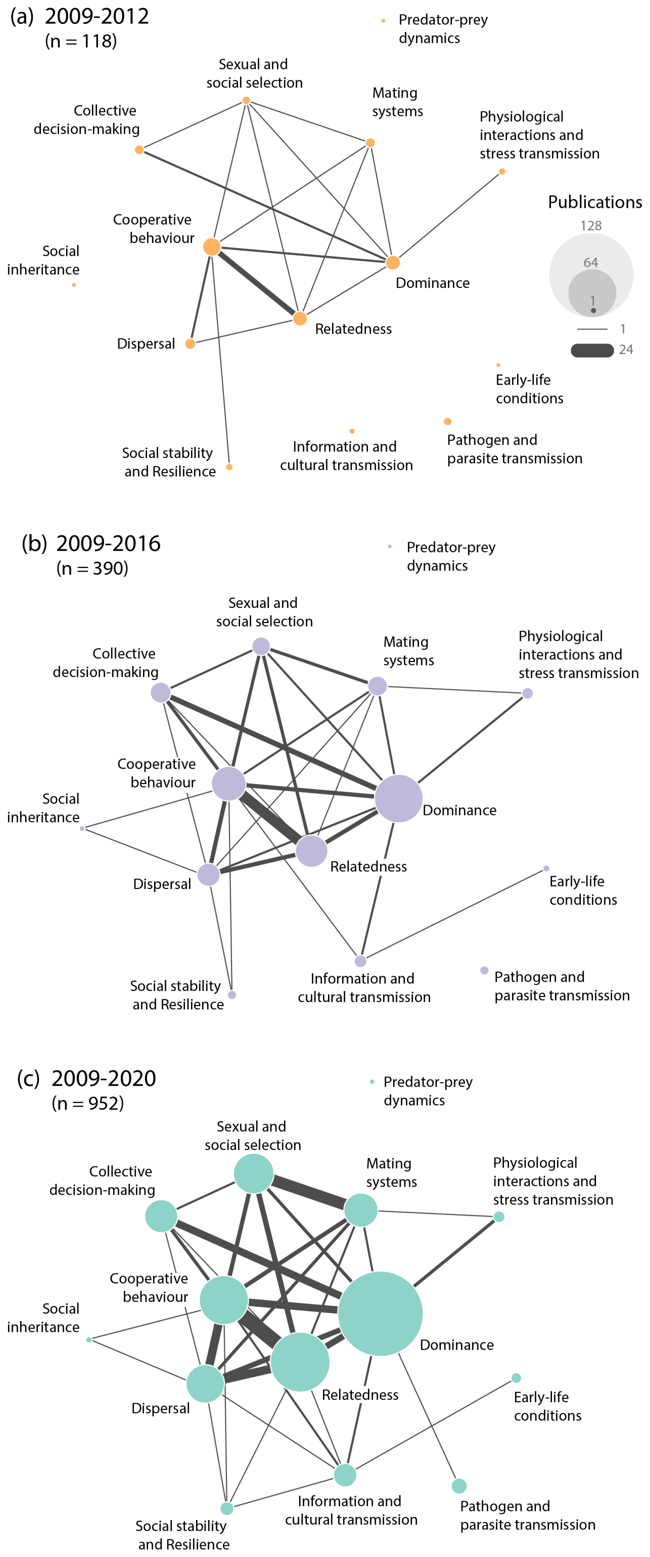

Figure 2. Strong, weak, and missing links among research topics on the ecology and evolution of animal social structure. Networks of co-occurrence of topics in original peer-

reviewed scientific articles between 2009 and 2020. Each node represents one of 14 research topics. Node sizes representing the number of articles that address that topic, while edge widths represent the number of articles where pairs of topics (i.e. the connected nodes) were addressed in the same article. The networks represent the accumulation of articles over three 4-year periods: (a) 118 articles published between 2009 to 2012, (b) 390 articles published from 2009 to 2016, and (c) 952 articles from 2009 to July 2020. See Box 1 and Supporting Information S1 for more information on how these networks were constructed.

Box 1. Identifying potential and realized connections in individual-to-society feedback loops

Over the past two decades, the two major perspectives in animal behaviour—the ethological approach concerned with its evolutionary causation and the behavioural ecology approach concerned with its functions and fitness consequences—have been bridged by network-thinking (Whitehead 2008). The bulk of work on causes and consequences of animal social structures, especially the recent cohort of studies inspired by network theory, have depicted social structure as being static, overlooking the inherent dynamism of any social system (Pinter-Wollman *et al.* 2014). Both individuals and societies are dynamic systems. Over time, societies can change in size and composition and the distribution of social relationships can be restructured (Shizuka & Johnson 2020). At the same time, each individual is in itself a dynamic system, changing states over time. For instance, through the course of their lives individuals learn from the environment and/or their peers (Kulahci & Quinn 2019), change in behavioural motivations as they cross life stages (e.g. Berman 1982), and grow in social competences as they mature within their social environments (Taborsky & Oliveira 2012). Thus, societies are rewired as new individuals enter and old ones change or leave; as new social ties are formed and old ones collapse. These social dynamics, when accounted for, are typically considered independently from one another, although they are best considered as bidirectional (Gross & Blasius 2008; Farine 2018).

Feedback loops between individuals and societies mean that the evolution of social structure and the state of the individuals reciprocally influence each other (Fig. 1). In this review, we look at linkages between multiple drivers of individual state and the processes influenced by social structure, and where new connections can be made. To highlight the strong existing connections and identify the general gaps in individual-to-society feedback loops, we reviewed the literature addressing causes and consequences of animal social structures.

We first identified 14 of the common and emerging research topics in the study of animal social structures, and then quantified how many publications addressed each topic together and separately (Fig. 2). Although the use of network methods in the field of animal behaviour dates back to the 1970's (Brent, Lehmann & Ramos-Fernández 2011), our focus is on the last decade when the networks methodology gained popularity due to the publication of two influential books (Croft, James & Krause 2008; Whitehead 2008; Whitehead 2009; Croft *et al.* 2011; Farine & O'Hara 2013; Farine & Whitehead 2015). We based our search of original peer-reviewed papers by identifying the studies citing the most influential methodological (Croft, James & Krause 2008; Whitehead 2008; Whitehead 2009; Croft *et al.* 2011; Farine 2013; Farine & Whitehead 2015) and review papers (Wey *et al.* 2008; Krause, Lusseau & James 2009; Sih, Hanser & McHugh 2009; Pinter-Wollman *et al.* 2014) on animal social network analysis. We extracted the citations of these influential publications from the Web of Science database on the 10th of July 2020. The initial search yielded 1885 citations. After removing duplicates and 276 review articles and book chapters, we analysed a total of 952 original peer-reviewed articles. We then analysed the title and keywords of these articles to quantify which of them contained each of the 14 research topics (and closely-related terms, e.g. 'relatedness', 'kinship', 'kin'; see Supplementary Material 1). We then generated a network depicting edges as the co-occurrence of topics in the same articles (Fig. 2).

The cumulative publication networks revealed a core of well-connected research topics along with a set of more peripheral topics (Fig. 2). The most studied topics in the last 12 years include bottom-up drivers of individual states (e.g. 'relatedness', 'dominance'), while the top-down influences are usually underrepresented (e.g. 'social stability and resilience', 'early-life conditions'). Well-known cross-disciplinary research is represented by strong links (e.g. 'relatedness'—'cooperative behaviour', and 'mating systems'—'sexual and social selection'). The rapid increase in publications is clear from the accumulation of published articles by the end of each of the three period (2009-2012: n=118; 2009-2016: n=390; 2009-2020: n=936; Fig. 2). There was a visible increase in the network connectivity from 2009-2012 (connectivity = 18.7%) to 2009-2016 (33.0%), but this largely stagnated over the following years 2009-2020 (39.6%) even though the number of articles more than doubled (Fig. 2). These patterns suggest some branching out from the first to the second period, and greater focus on classical topics (e.g. 'dominance', 'cooperative behaviour'), and somewhat less exploitation of new areas in the last period. Some exceptions are 'cultural transmission' and 'social stability and resilience', whose degrees increased from 0 to 7 and 1 to 4, respectively.

Importantly, our analysis reveals that there are still under-represented and weakly-connected topics, revealing promising areas for further cross-disciplinary research. Among the missing links, we highlight (i) the completely disconnected topic 'predator-prey dynamics'; (ii) the potential links from 'social inheritance' to 'dominance', to 'relatedness' and to 'information and cultural transmission'; and (iii) all potential links among the topics 'early-life conditions', 'dispersal', 'social stability' and 'physiological interactions and stress transmission'. Among the weak links, we highlight (iv) those to and from 'social stability and resilience', (v) links from 'social inheritance' to 'dispersal', as well as (vi) links from 'pathogen and parasite transmission' to ‘dominance’ and to ‘physiological interactions’. We discuss these prominent areas for future research in the “Future prospects for studying individual-to-society feedbacks” section.

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