The evolutionary and ecological consequences of animal social networks: emerging issues

Ralf H.J.M. Kurvers[1]*, Jens Krause[1,2]*, Darren P. Croft[3], Alexander D.M. Wilson[1], and Max Wolf[1]

[1] Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Mueggelseedamm 310, 12587 Berlin, Germany
[2] Humboldt University of Berlin, Faculty of Life Sciences, Invalidenstraße 42, 10115 Berlin, Germany
[3] Centre for Research In Animal Behaviour, College of Life & Environmental Science, University of Exeter, Exeter, EX4 4QG, UK

The first generation of research on animal social networks was primarily aimed at introducing the concept of social networks to the fields of animal behaviour and behavioural ecology. More recently, a diverse body of evidence has shown that social fine structure matters on a broader scale than initially expected, affecting many key ecological and evolutionary processes. Here, we review this development. We discuss the effects of social network structure on evolutionary dynamics (genetic drift, fixation probabilities, and frequency-dependent selection) and social evolution (cooperation and between-individual behavioural differences). We discuss how social network structure can affect important co-evolutionary processes (host–pathogen interactions and mutualisms) and population stability. We also discuss the potentially important, but poorly studied, role of social network structure on dispersal and invasion. Throughout, we highlight important areas for future research.

Population social structure

The social structure of animal groups and populations has been a long-standing topic in biological research [1,2]. Approximately 10 years ago, social network analysis entered behavioural biology [3–5] and provided a new way of investigating animal social structure (see Box 1 for a brief introduction to animal social networks). Social network analysis (see Glossary) has promoted an understanding of the social fine structure of groups, communities, and entire populations, thereby generating new insights into the complex social structures in which individuals are embedded and the selection pressures that shape their behaviour [6–10]. Social network analysis has now become widely accepted as an important conceptual framework for studying social interactions in animal groups [11–15]. It has found applications in all major taxa [8,9,16,17] and has added significantly to the understanding of major biological processes ranging from disease and information transmission [7,16] to cooperation [6,18] to sexual selection [10].

Network analysis entered organismal biology mainly via the social sciences. As a result, the first generation of research on animal social networks was primarily

Glossary

Average path length: the average shortest distance between all possible pairs of nodes in a network. Low values mean that, on average, few connections are needed to connect two nodes, implying high transmission efficiency through a network.

Clustering coefficient: a measure of how tightly nodes are clustered in a network. This can apply to a node (local clustering coefficient) or a network (global clustering coefficient). The local clustering coefficient quantifies the extent to which the immediate neighbours of a node are themselves neighbours. The global clustering coefficient of a network is the average of all local clustering coefficients.

Degree: the number of direct ties (paths of length one) between a focal node and other nodes.

Degree distribution: the frequency distribution of the degrees of all nodes in a network.

Interaction network: the network that describes who interacts with whom in fitness-determining interactions.

Network: a collection of nodes connected by zero or more ties.

Network density: the ratio of existing ties to the number of all possible ties in a network.

Node (or vertex): along with ties, one of the basic elements of a network. Nodes are connected in a network by ties. In animal social networks, nodes usually represent individuals.

Random network: a network where the edges between nodes are placed randomly.

Regular network: a network in which each node has the same degree.

Replacement network: a network where each node represents a breeding individual and each tie represents offspring dispersal; that is, the chance that an offspring born at one of the connected nodes displaces the breeding individual at the other node.

Scale-free network: a network in which the degree distribution follows a power law implying that most nodes have a low degree and few nodes have a very high degree.

Small-world network: a network in which (for a fixed mean degree) the average path length increases logarithmically or slower with the number of nodes in the network. Small-world networks are characterised by a high global clustering coefficient and a short average path length.

Tie (or edge): along with nodes, one of the two basic elements of a network, representing an interaction process between nodes. In animal social networks, these interactions include, but are not limited to, affiliative, aggressive, cooperative, and sexual interactions.

Well-mixed population: a population where all pairs of individuals have equal probabilities of interacting with each other corresponding to a complete graph with network density one.

Box 1. A brief introduction to animal social networks

Animals often interact nonrandomly with group members, which can give rise to complex social relations that can be described by a SNS comprising nodes (representing individuals) connected by ties (representing an interaction between two individuals). Animal social networks are multidimensional [88] and dynamic [13]. Animals typically interact with their group members in multiple different contexts. Animals can, for example, interact in affiliative, aggressive, cooperative, and mating networks with the same or different individuals. Individual preferences for associations can be different between contexts [89], leading to different SNS in different contexts. There can be carryover effects between different contexts, whereby interactions in one context have consequences for the network structure in another context [14]. Furthermore, associations between individuals and, thus, SNS can change over space and time as individuals break ties and form new social ties in response to, for example, environmental conditions, internal states, and previous social experiences [13]. As discussed in this review, SNS can have important consequences for ecological and evolutionary processes and we briefly introduce three conceptually important network structures (Figure I). In a regular network, all individuals have the same degree (i.e., number of social interaction partners). In the particular regular network shown in Figure I, all individuals interact with their four nearest neighbours and the network has a high clustering coefficient and a long average path length. A few random changes in tie connections (rewiring) give rise to a small-world network. Small-world networks are also highly clustered, but due to the existence of long-distance connections, they are characterised by a short average path length, increasing the interconnectedness of the network. For large rewiring probabilities, the network turns into a random network (see [90] for a discussion on different rewiring procedures). A random network is characterised by a low clustering coefficient and a short average path length.
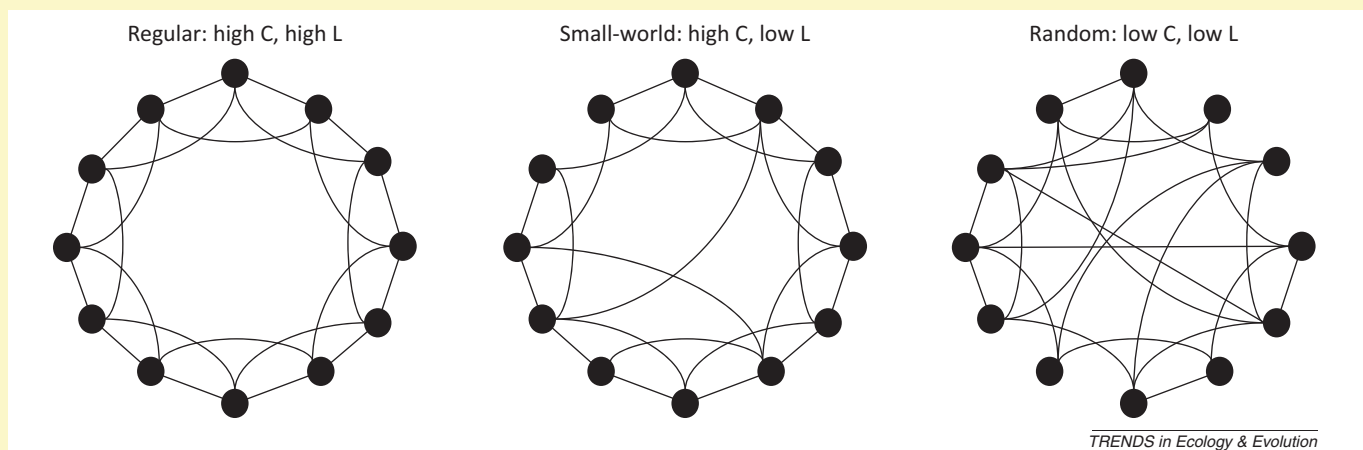

Figure I. Three conceptually important network structures. All networks have the same number of nodes and ties. Abbreviations: C, clustering coefficient; L, average path length. Modified from [65].

focussed on issues that social scientists designed it for, such as information transmission, social cohesion, and cooperation [12,14,15]. However, more recently, evidence has been accumulating that population social structure matters on a broader scale, affecting a diverse range of ecological and evolutionary processes. Here, we review this development and outline promising areas for future research. In particular, we focus on six emerging topics that connect population social structure with key evolutionary and ecological processes. We start by discussing the importance of social network structure (SNS) for three fundamental evolutionary topics (evolutionary dynamics, social evolution, and coevolution). We then proceed by discussing how SNS affects three major ecological topics (population stability, dispersal, and invasion). Although the primary focus of this article is thus on the consequences of SNS for key evolutionary and ecological processes, we also consider the various ways that these processes feedback on the SNS.

Evolutionary dynamics

Two important aspects of SNS are the network of fitness-determining interactions (aka 'interaction network') and the structure of dispersal of offspring (aka 'replacement network') [19]. A growing body of recent theoretical research suggests that the fine structure of these networks can have substantial consequences for evolutionary dynamics and evolutionary outcomes.

First, genetic drift is predicted to depend on SNS [20,21]. In particular, when comparing regular-, to small world-, to random-, to scale-free replacement networks, the mean time to loss of neutral variation decreases [21]. Thus, decreasing the regularity of the replacement network tends to decrease the time to loss of neutral variation, the reason being that, in more regular networks, different parts of the population are more distantly connected to each other, therefore preserving different alleles more easily.

Second, SNS is predicted to affect the fixation probability of new mutations and the time to fixation of such mutations (see also the discussion of frequency-dependent selection below). The fixation probability of a mutant depends both on the structure of the local network around that mutant and the global structure of the network [20,22]. In regular replacement networks, the fixation probability of a mutant does not depend on its starting position [20,22]. When comparing a large number of irregular replacement networks, the fixation probability has been found to decrease with the degree of the node where it is introduced [22]. This is because the chance that a mutant at a particular node gets replaced increases with the degree of that node. Comparing different global network

structures, some replacement networks have been found to amplify selection (i.e., increase the fixation probability of advantageous mutations and decrease those of disadvantageous mutations), whereas others have the reverse effect [20,22]. It appears that the degree variance of the replacement network has a key role here, networks with a higher variance (e.g., star-structured networks) tend to amplify selection, whereas more regular networks tend to have the reverse effect [20,22]. Interestingly, although high-degree variance can amplify selection, it also tends to increase time to fixation, because a higher-degree variance is associated with fewer routes to fixation [22–24].

Third, SNS affects the dynamics and outcome of frequency-dependent selection. In particular, the fundamental equation of evolutionary game dynamics, the replicator equation, and the conditions for evolutionary stability have been shown to depend systematically on the properties of SNS [20,25,26]. This is because the evolutionary fate of a particular strategy under frequency-dependent selection depends on the strategy of its interaction partners, which (whenever there is some variation in the population) is affected by SNS. A key aspect here is whether and to what extent SNS promotes that individuals that use the same strategy tend to interact with each other [27], a phenomenon known as 'homophily'; cooperators, for example, tend to be evolutionary competitive only in networks that promote the clustering of types [6] (see also the section entitled 'Social evolution').

Finally, although we have stressed the effect of SNS on evolutionary dynamics, similar principles can be expected to apply to cultural dynamics governed by social learning. In fact, several of the above-discussed studies (e.g., [20,25,26]) explicitly address cultural dynamics (see also [28]). Following the arguments above, the mean time to loss of neutral cultural variants is expected to decrease as the regularity of the SNS decreases [21] and the outcome of frequency-dependent cultural selection should depend on the degree to which SNS promotes the clustering of cultural variants [27].

Social evolution

A key factor in social evolution is the social environment that individuals are confronted with. Here, we discuss two main ways by which SNS affects the evolution of social behaviour via the social environment.

First, SNS affects the evolution of cooperation. Although selfish individuals are favoured in well-mixed populations, cooperation can become evolutionary competitive when SNS promotes the clustering of strategy types [6]. This is because such clustering makes cooperators more likely to interact with other cooperators, thereby increasing the fitness of cooperators. Recent theoretical [29,30] and empirical [18,31,32] studies have investigated situations where individuals could not only adjust their cooperativeness, but were also allowed to break off the interaction and form new social ties. Interestingly, such coevolution of network structure and behaviour appears to be a powerful mechanism promoting social structures that favour high levels of cooperation. In an experiment with humans, for example, Fehl *et al.* [18] found that these dynamic networks give rise to cooperative clusters of individuals where

cooperativeness is positively correlated with the clustering coefficient of individuals.

Second, SNS can have a key role in shaping both the amount of behavioural variation present in a population and how that variation is distributed among individuals. SNS often gives rise to between-individual differences in social environments and social experiences [14,33] that, in turn, can select for between-individual differences in social behaviour. The higher the number of interaction partners, and the higher the variation between those partners, the more socially responsive and choosy an individual should be [14,34]. For example, the more high-quality males a female encounters, the more willing she should be to reject a low-quality male [14]; in cooperative interactions, choosiness is only beneficial if there is sufficient variation between social partners [35]. SNS can also promote systematic between-individual differences in fitness expectations (i.e., residual reproductive value). For example, orderly (i.e., transitive) dominance networks [36] can give rise to between-individual differences in reproductive success [37], and the risk of an individual to become infected with a disease or parasite depends on the structure of its contact network [38–40]. Differences in fitness expectations, in turn, are predicted to promote differences in all kinds of risk-related behaviour where individuals with high expectations are predicted to be more cautious (i.e., less willing to put their life at danger for a given benefit, aka 'asset protection principle') compared with individuals with low expectations [41,42].

Although the evolution of social behaviour is thus affected by SNS, social behaviour feeds back on that structure. These feedbacks are mediated by social responsiveness, which is the tendency to break and form new social ties, dependent on past social experience. Whether an individual should be socially responsive depends on its social environment (see above); social responsiveness, in turn, directly changes this social environment and, thus, the emerging SNS. This is illustrated by the above-discussed studies on the coevolution of network structure and cooperation [18,31,32], where the very network structure that promotes cooperation is created by the social responsiveness of individuals.

Coevolution

We have seen that SNS can profoundly influence evolutionary dynamics and social evolution. Thus, it should come as no surprise that SNS can affect coevolutionary processes in which two or more species affect each other's evolution. Here, we discuss the role of SNS in host–pathogen interactions, the evolution of restraint, and mutualism.

In host–pathogen interactions, the SNS of the host can affect virulence and transmissibility of pathogens, and host resistance. Theory predicts that sparse host contact networks (i.e., low average degree) select for reduced pathogen virulence because transmission is more difficult in sparse networks, forcing pathogens to treat their host more carefully [43]. Furthermore, the higher the clustering coefficient and the longer the average path length of the host SNS, the stronger the selection for reduced transmission rates and virulence [43,44]. This is because pathogens with high transmission rates and high virulence would quickly

infect all individuals in their local environment, increasing competition for themselves ('self-shading') and for their kin ('kin-shading') [45]. In agreement, Boots and Mealor [46] showed experimentally that more localised interactions in the host population selected for lower pathogen infectivity. The SNS of the host can also affect the evolution of host resistance. Theoretical research predicts that high clustering of the replacement network of the host (i.e., the host reproduces locally) selects for increased host resistance [47]. This is because mutants with increased resistance are more likely to be surrounded by other mutants with increased resistance, thereby benefiting from regions of low parasite prevalence. Finally, given that many social animals have evolved strategies to reduce contact with infected individuals [48], pathogen infection patterns can feed back on the SNS of the host. For example, Croft *et al.* [49] introduced either infected or uninfected guppies, *Poecilia reticulata*, into groups of guppies. Infected individuals spent less time shoaling than uninfected individuals because group members initiated more shoal-splitting events in the presence of infected individuals. As a consequence, the network of groups containing infected individuals showed reduced clustering, illustrating how infection can change the SNS of the hosts.

SNS also has an important role in the evolution of restraint (i.e., a strain or species does not evolve to its maximum competitive ability). Theoretical studies predict that, in communities with intransitive competitive relations (e.g., A outcompetes B, B outcompetes C, and C outcompetes A), high clustering (i.e., local interactions) favours the evolution of restraint [50,51]. Whenever A evolves to a more rapacious form A*, B decreases in abundance, which increases the abundance of C, lowering the abundance of A*. This negative feedback favours the evolution of restrained competitors when interactions are predominantly local. When interactions become global, selection for restraint is weakened because unrestrained individuals can escape the negative consequences of their overexploitation [50,51]. In agreement with this prediction, Nahum *et al.* [52] found that limiting migration of three strains of *Escherichia coli* with intransitive relations resulted in evolved restraint (for similar findings, see [46,53]).

SNS can also affect mutualistic interactions. Several theoretical studies predict that well-mixed populations disfavour mutualism, whereas structured populations favour mutualism [54,55]. For example, Doebeli and Knowlton [54] investigated a situation where hosts and symbionts were placed on separate but identical lattices. Each host interacted with the symbiont on the same grid point of the other lattice and the fitness of hosts and symbionts was determined by both the host–symbiont interaction and local within-species competition. Under these conditions, mutualism evolved because similar strategies are more likely to interact with each other, promoting clusters of mutualistic interactions. Thus, SNS can affect mutualism, but mutualism is also predicted to affect the SNS. Mack [56] simulated the coevolution of mutualism and dispersal distance and found that such coevolution resulted in a shorter dispersal distance of mutualists compared with nonmutualists, thereby promoting a SNS that favours mutualism.

Population stability

A key issue in community ecology is how the structure of species networks affects the stability, resilience, and robustness of these networks (e.g., [57]). By contrast, comparatively few studies have investigated how SNS affects the stability of populations. We here discuss two main ways that link SNS with population stability.

First, SNS is predicted to mediate whether and to what extent a population fragments in response to the removal of individuals [58]. In networks where all individuals have approximately the same number of social contacts (e.g., regular networks), the removal of any individual causes a similar decrease in interconnectedness (i.e., increase in average path length) of the population [58]. By sharp contrast, in networks where most individuals have few but some individuals have a large number of social contacts (e.g., scale-free networks), interconnectedness is predicted to change little in response to the random removal of individuals (because most individuals have only few social contacts), but a large decrease in interconnectedness is predicted in response to the removal of even a small fraction of the highly connected individuals (assuming that these individuals do not get replaced) [58]. Although these predictions are in line with the outcome of simulated removal studies in killer whales [59], ground squirrels [60], and chimpanzees [61], few studies thus far have investigated the consequences of true removal of individuals. In one such study, Flack *et al.* [62] found that, in a captive group of pigtailed macaques, *Macaca nemestrina*, the targeted 'knockout' of a small number of individuals associated with the policing function resulted in smaller and less integrated social interaction networks (i.e., networks with a decreased average degree and an increased clustering coefficient).

Second, theoretical research predicts that SNS is a key determinant of the vulnerability of populations to infectious diseases and pathogens [7,63–65]. Transmission dynamics are more rapid in more dense social networks where individuals have a higher number of social contacts. High clustering can reduce the early growth rate of infections, because clustering promotes local interactions where infected individuals tend to deplete the susceptible individuals in their local environment [7]. Increased interconnectedness (i.e., decreased average path length) decreases the likelihood that an epidemic is contained in small parts of the population, because previously isolated parts of the population become interconnected [65]. Finally, in scale-free networks, the highly connected individuals (termed 'super-spreaders') have a key role in the maintenance and spread of infections [7]. Until now, few field studies have investigated these theoretical predictions. In line with the above predictions, in the social bumble bee, *Bombus impatiens*, among-colony differences in rates of infection with a contagious pathogen resulted largely from differences in network density among hives [66], whereas the prevalence of the parasite, *Cryptosporidium* spp. in two geographically separated colonies of the Belding's ground squirrel, *Spermophilus beldingi*, was negatively correlated with the clustering coefficient [40].

## Box 2. The importance of social network position for dispersal

Yellow-bellied marmots (*Marmota flaviventris*) (Figure I) are facultative social rodents. In this species, approximately half of the yearling females disperse from the colony, whereas nearly all yearling males disperse [73]. This male-biased dispersal is reflected in sex-specific differences in the importance of affiliative network positions. In yearling females, individuals that were well embedded in the affiliative network were less likely to disperse. In yearling males, there was no effect of network position on dispersal decisions [73] (Figure II).

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Figure I. Two yellow-bellied marmot pups playing near their parent. Reproduced, with permission, from Ben Hulsey.
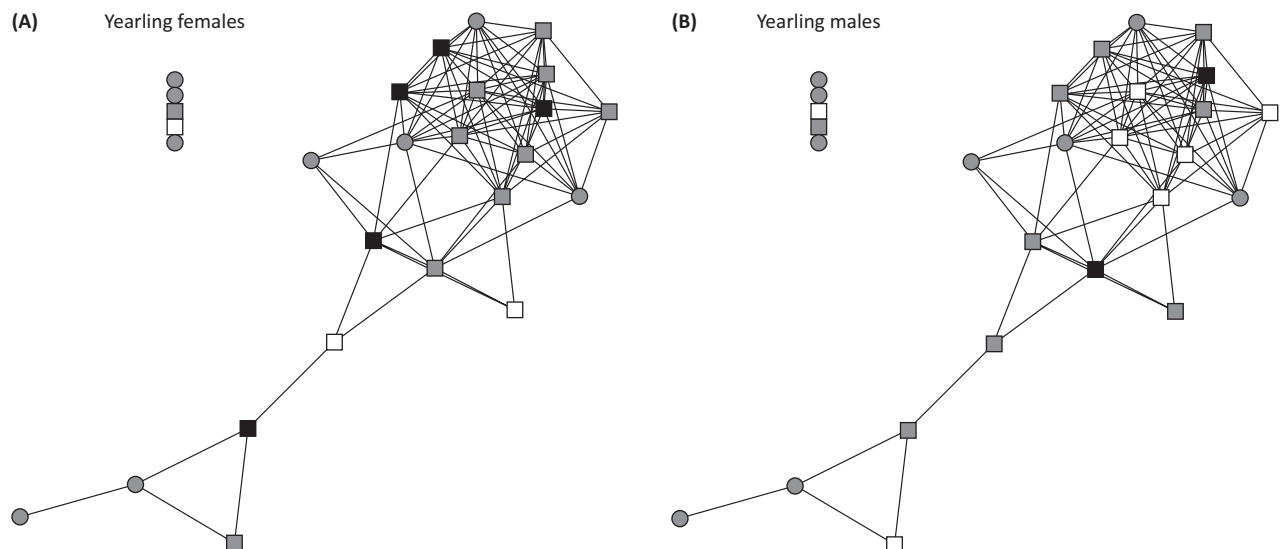
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Figure II. Illustrations of two networks derived from affiliative behaviours between yellow-bellied marmots. Squares represent yearlings, circles represent adults, white represents dispersers, black represents nondispersers, and grey represents all other individuals. (A) In the female network, dispersers (white squares) are at the periphery of the network, meaning that they have low embeddedness (i.e, are not well integrated in the network [91]). (B) By contrast, the male network shows no difference in dispersal according to embeddedness, as shown by the scattered distribution of white squares throughout the network [73]. Reproduced, with permission, from Dan Blumstein.

Dispersal

Identifying the key factors that drive dispersal has been a long-standing topic in ecological research. Several factors have been identified, including kin competition, inbreeding avoidance, resource competition, and parasitism [67,68]. However, the role of SNS on dispersal has rarely been studied. Here, we discuss three ways in which SNS can affect adaptive dispersal decisions via the above-mentioned factors.

First, optimal dispersal decisions are affected by the relatedness of an individual with its interaction partners. The overall effect of relatedness on dispersal depends on the relatedness experienced in several different interaction networks. The higher the relatedness in competitive interaction networks, the higher the pressure to disperse, because this places the burden of competition on nonkin [69]. The higher the relatedness in cooperative and affiliative interaction networks, the lower the pressure to disperse, because high relatedness promotes cooperation [70]. Finally, the higher the relatedness in the mating network, the higher the pressure to disperse to avoid inbreeding [71].

Second, irrespective of kin, the local SNS at the natal site can affect the expected costs and benefits of staying at the natal site. Under the 'social cohesion hypothesis' [72],

individuals that are better embedded in the affiliative social network are expected to have a lower dispersal tendency because they suffer less from intraspecific competition and aggression. In line with this prediction, yearling female yellow-bellied marmots, *Marmota flaviventris*, that were more socially embedded in the affiliative network were less likely to disperse [73] (Box 2). Similar findings were reported from blue monkeys, *Cercopithecus mitis*, and house mice, *Mus musculus* [74,75].

Third, optimal dispersal decisions depend on the risk of becoming infected with a disease or parasite [68], which, in turn, depends on the structure of the local network around an individual and the global SNS. Theoretical studies predict that the risk of infection increases with an individual's degree [38] and, in agreement, several studies have

Table 1. Evolutionary and ecological implications in a nutshell

	Implications
Evolutionary dynamics	The time to loss of neutral variation is predicted to decrease with decreasing regularity of the replacement network
	The fixation probability of a mutation in a replacement network is predicted to decrease with the degree of the node where it is introduced
	The fixation probability of an advantageous (disadvantageous) mutation is predicted to increase (decrease) with the degree variance of the replacement network
	The time to fixation of a mutation is predicted to increase as the degree variance of the replacement network increases
	The dynamics and outcome of frequency-dependent selection depend on whether and to what extent SNS promotes that individuals that use the same strategy tend to interact with each other
Social evolution	SNS can promote (inhibit) the evolution of cooperation via promoting (inhibiting) the clustering of strategy types (i.e., cooperative individuals are more likely to interact with other cooperators)
	SNS can promote between-individual differences in behaviour: (i) the higher the number of interaction partners and the larger the variation between these partners, the more choosy and/or socially responsive an individual is predicted to be; (ii) differences in contact networks can give rise to differences in future fitness expectations that, in turn, are predicted to promote differences in all kinds of risk-related behaviour
Coevolution	SNS of hosts can affect the virulence and transmission rate of pathogens and host resistance: (i) dense host networks select for reduced pathogen virulence; (ii) high clustering and high average path length of the host network select for reduced transmission rates and reduced virulence; (iii) host resistance increases with increased clustering of the host replacement network
	Infections can reduce clustering in the host network
	The evolution of restraint is favoured in highly clustered competitor networks, whereas the evolution of mutualism is favoured in highly clustered networks of hosts and symbionts
Population stability	SNS can mediate population fragmentation in response to the removal of individuals: (i) when all individuals have approximately the same number of social contacts, each individual is predicted to cause a similar decrease in population interconnectedness (i.e., increase in average path length) when removed; (ii) when most individuals have few but some individuals have a large number of social contacts, interconnectedness changes little with the random removal of individuals, but large decreases in interconnectedness are predicted in response to the targeted removal of highly connected individuals
	SNS can affect the vulnerability of populations to infectious diseases and parasites: (i) transmission dynamics are more rapid in more dense networks; (ii) high clustering reduces early growth rate of infections; (iii) increased interconnectedness (i.e., decreased average path length) decreases the likelihood that an epidemic is contained in small parts of the population; (iv) in scale-free networks, the highly connected individuals have a key role in the maintenance and spread of infections
Dispersal	SNS affects the relatedness of an individual with its interaction partners at the natal site, which can affect dispersal: (i) high relatedness in competitive interactions increases dispersal; (ii) high relatedness in cooperative interactions decreases dispersal; (iii) high relatedness in mating interactions increases dispersal
	Individuals that are well embedded in the affiliative network at the natal site have a lower dispersal tendency
	SNS at the natal site affects disease and parasite risk, which, in turn, is predicted to affect dispersal: (i) individuals with a high degree have a higher infection risk and are expected to have a higher dispersal tendency; (ii) more-dense contact networks result in higher parasite prevalence, which is predicted to increase the average dispersal tendency; (iii) high clustering reduces parasite prevalence, which is predicted to decrease the average dispersal tendency
Invasion	Well-connected invaders have better access to information, which is predicted to increase their invasion success
	The extinction risk of parasites following their host upon invasion is predicted to increase in sparser and/or more clustered host networks

Box 3. Ecological species networks and social networks

Ecological network studies typically use the species as unit of analysis, with ties representing different types of interaction (e.g., mutualistic or agonistic) [92,93]. The logistics of empirical studies of food webs or pollinator communities are a major challenge, even if relatively small numbers of different species are involved, thereby constraining the level of detail at which data can be collected. However, given that individual variation is one of the main drivers for evolutionary change [94], ecological networks might benefit from analysis at the level of individuals that would show the importance of individual attributes for emergent, population-level phenomena [95,96]. Such an approach could have major implications for the predictive power of network models that investigate how ecosystems respond to global change and how species extinctions will affect the rest of the system. Network analyses of information and disease spreading have shown that the existence of super-spreaders can be highly influential in transmission processes in some populations [7,64]. If the same were true, for example, in the context of pollination (i.e., that a small number of individuals accounts for a disproportionately large amount of pollination events) then the presence (or absence) of such individuals in pollination networks could make a considerable difference for the persistence of some species.

An individual-based approach to multispecies networks is facilitated by new technologies that allow, in some cases, the automated recognition of individuals in the field based on visual data ([97]; Figure I) and in others, the attachment of tags to individuals of entire groups or populations ([98]; Figure II). Studies that track association patterns of large numbers of individuals with multi- or even subsecond sampling rates have the potential to converge (within obvious limits) onto the ultimate goal of mapping biological 'reality'. Next to monitoring individual associations, field biologists increasingly use miniature animal-attached sensors that can aid in the remote collection of data about the physiology and/or environment of an animal. This powerful approach has become known as 'reality mining' [98] and biologists will soon be able to record field data sets of animal social behaviour and ecology of unprecedented size and quality.

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Figure II. Great tit, *Parus major*, equipped with an Encounternet tag [100]. Reproduced, with permission, from Lysanne Snijders.

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Figure I. Recent advances in animal biometrics make automated recognition possible for several species. This has resulted in online databases, such as the ECOCEAN Whale Shark Photo-identification library [99]. Reproduced, with permission, from Rodrigo Friscione Wyssmann.

shown that well-connected individuals were more infected by parasites compared with less-connected individuals [76,77]. This is predicted to have consequences for dispersal decisions, but to date there are no empirical studies linking individual network position, infection rates, and dispersal. Moreover, sparsely connected SNS and clustered SNS are predicted to have lower parasite prevalence (see also the section entitled 'Population stability') and, thus,

are expected to have lower levels of dispersal. Again, however, no field studies have yet investigated the relation between SNS, parasite prevalence, and dispersal across different populations.

Invasion

A key question in invasion ecology is which factors determine whether an invasion will be successful [78]. Up to

now, the role of SNS for invasion success has received surprisingly little attention. Here, we discuss two ways in which SNS can affect invasion success.

First, SNS affects flow processes within populations [11,12], which can affect invasion success in two ways: by affecting the information available to individuals, and by affecting the evolutionary response of a population. Individuals entering a novel habitat often lack important information on resources, refuge locations, and predators. The position of an individual within the SNS, in turn, can affect its access to information. Individuals with a high number of social interactions are, for example, better at discovering new food patches [79], leading to the prediction that well-connected individuals have an advantage in novel environments. In agreement, translocated African elephants, *Loxodonta africana*, with a higher degree in their novel environment, were in a better condition than translocated elephants with a lower degree [80]. A study on the invasive sunbleak, *Leucaspius delineatus*, showed that this species is highly interconnected with other fish species in its novel environment, suggesting that successful invasion is partly due to integration in the local social systems [81]. Next to affecting the information available to individuals, the SNS of an invading population affects its evolutionary responses (see the section entitled 'Evolutionary dynamics'), which, in turn, are known to be an important factor mediating invasion success [82].

Second, the invasion success of host species is often attributed to a release from a regulatory effect of parasites in their native range (the 'enemy release hypothesis') [83]. If the parasite arrives with its host in a new habitat, its potential to spread and survive in this habitat is expected to depend on the SNS of the host [84]. In sparse host contact networks, where individuals tend to have few social contacts, the parasite runs a greater risk of going extinct because of limited opportunities for transmission [84,85]. Similarly, in highly clustered networks, parasites tend to deplete the susceptible individuals in their local neighbourhood, thereby increasing the likelihood of parasite extinction [85] (see also the section entitled 'Population stability').

Population social structure: a fundamental biological dimension

Much previous research on animal social networks focussed on a limited number of contexts, such as information and disease transmission and cooperation. Here, we have reviewed the recently accumulating evidence that population social structure affects a broader range of ecological and evolutionary processes (Table 1) and we hope that our work inspires further research into these and related areas. Next to the issues discussed above, promising topics for future research include the consistency of social network position over the lifetime of an individual (in which case, social network position becomes an integral part of the social personality of an individual) [86], the heritability of social network positions [87], and trade-offs associated with different social network positions and different social network structures. Finally, a closer integration of ecological species networks and social networks

is a promising avenue for future research, especially in the light of new technological developments (Box 3).

In some contexts, such as information and disease transmission, and cooperation, the importance of population social structure has been firmly established. However, as highlighted by this review, social structure links mechanistic and functional aspects on a broader scale. Thus, population social structure can be identified as one of the fundamental biological dimensions that affects a wide range of ecological and evolutionary processes.

References

1 Hinde, R.A. (1976) Interactions, relationships and social structure. *Man* 11, 1–17
2 Wilson, E.O. (1975) *Sociobiology: the New Synthesis*, Harvard University Press
3 Croft, D.P. *et al.* (2004) Social networks in the guppy (*Poecilia reticulata*). *Proc. Biol. Sci.* 271, S516–S519
4 Lusseau, D. (2003) The emergent properties of a dolphin social network. *Proc. Biol. Sci.* 270, S186–S188
5 Ward, A.J.W. *et al.* (2002) Association patterns and shoal fidelity in the three-spined stickleback. *Proc. Biol. Sci.* 269, 2451–2455
6 Ohtsuki, H. *et al.* (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441, 502–505
7 Keeling, M.J. and Eames, K.T.D. (2005) Networks and epidemic models. *J. R. Soc. Interface* 2, 295–307
8 Lusseau, D. and Newman, M.E.J. (2004) Identifying the role that animals play in their social networks. *Proc. Biol. Sci.* 271, S477–S481
9 McDonald, D.B. (2007) Predicting fate from early connectivity in a social network. *Proc. Natl. Acad. Sci. U.S.A.* 104, 10910–10914
10 McDonald, G.C. *et al.* (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philos. Trans. R. Soc. B* 368, 20120356
11 Croft, D.P. *et al.* (2008) *Exploring Animal Social Networks*, Princeton University Press
12 Krause, J. *et al.* (2007) Social network theory in the behavioural sciences: potential applications. *Behav. Ecol. Sociobiol.* 62, 15–27
13 Pinter-Wollman, N. *et al.* (2013) The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* 25, 242–255
14 Sih, A. *et al.* (2009) Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* 63, 975–988
15 Wey, T. *et al.* (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75, 333–344
16 Allen, J. *et al.* (2013) Network-based diffusion analysis reveals cultural transmission of lobtail feeding in Humpback whales. *Science* 340, 485–488
17 Fewell, J.H. (2003) Social insect networks. *Science* 301, 1867–1870
18 Fehl, K. *et al.* (2011) Co-evolution of behaviour and social network structure promotes human cooperation. *Ecol. Lett.* 14, 546–551
19 Ohtsuki, H. *et al.* (2007) Evolutionary graph theory: breaking the symmetry between interaction and replacement. *J. Theor. Biol.* 246, 681–694
20 Lieberman, E. *et al.* (2005) Evolutionary dynamics on graphs. *Nature* 433, 312–316
21 Whigham, P.A. *et al.* (2008) Genetic drift on networks: ploidy and the time to fixation. *Theor. Popul. Biol.* 74, 283–290
22 Broom, M. *et al.* (2011) Evolutionary dynamics on graphs: the effect of graph structure and initial placement on mutant spread. *J. Stat. Theory Pract.* 5, 369–381

23 Frean, M. *et al.* (2013) The effect of population structure on the rate of evolution. *Proc. Biol. Sci.* 280, 20130211

24 Voelkl, B. (2010) The 'Hawk-Dove' game and the speed of the evolutionary process in small heterogeneous populations. *Games* 1, 103–116

25 Ohtsuki, H. and Nowak, M.A. (2008) Evolutionary stability on graphs. *J. Theor. Biol.* 251, 698–707

26 Ohtsuki, H. and Nowak, M.A. (2006) The replicator equation on graphs. *J. Theor. Biol.* 243, 86–97

27 Tarnita, C.E. *et al.* (2009) Strategy selection in structured populations. *J. Theor. Biol.* 259, 570–581

28 Cantor, M. and Whitehead, H. (2013) The interplay between social networks and culture: theoretically and among whales and dolphins. *Philos. Trans. R. Soc. B* 368, 20120340

29 Pacheco, J.M. *et al.* (2006) Active linking in evolutionary games. *J. Theor. Biol.* 243, 437–443

30 Santos, F.C. *et al.* (2006) Cooperation prevails when individuals adjust their social ties. *PLoS Comput. Biol.* 2, 1284–1291

31 Rand, D.G. *et al.* (2011) Dynamic social networks promote cooperation in experiments with humans. *Proc. Natl. Acad. Sci. U.S.A.* 108, 19193–19198

32 Wang, J. *et al.* (2012) Cooperation and assortativity with dynamic partner updating. *Proc. Natl. Acad. Sci. U.S.A.* 109, 14363–14368

33 Krause, J. *et al.* (2010) Personality in the context of social networks. *Philos. Trans. R. Soc. B* 365, 4099–4106

34 McNamara, J.M. and Leimar, O. (2010) Variation and the response to variation as a basis for successful cooperation. *Philos. Trans. R. Soc. B* 365, 2627–2633

35 McNamara, J.M. *et al.* (2008) The coevolution of choosiness and cooperation. *Nature* 451, 189–192

36 McDonald, D.B. and Shizuka, D. (2013) Comparative transitive and temporal orderliness in dominance networks. *Behav. Ecol.* 24, 511–520

37 Ellis, L. (1995) Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol. Sociobiol.* 16, 257–333

38 Christley, R.M. *et al.* (2005) Infection in social networks: using network analysis to identify high-risk individuals. *Am. J. Epidemiol.* 162, 1024–1031

39 Godfrey, S.S. (2013) Networks and the ecology of parasite transmission: a framework for wildlife parasitology. *Int. J. Parasitol. Parasites Wildl.* 2, 235–245

40 VanderWaal, K.L. *et al.* (2013) Network structure and prevalence of *Cryptosporidium* in Belding's ground squirrels. *Behav. Ecol. Sociobiol.* 67, 1951–1959

41 Clark, C.W. (1994) Antipredator behavior and the asset-protection principle. *Behav. Ecol.* 5, 159–170

42 Wolf, M. *et al.* (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447, 581–584

43 van Baalen, M. (2002) Contact networks and the evolution of virulence. In *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management* (Dieckmann, U. *et al.*, eds), pp. 85–103, Cambridge University Press

44 Boots, M. and Sasaki, A. (1999) 'Small worlds' and the evolution of virulence: infection occurs locally and at a distance. *Proc. Biol. Sci.* 266, 1933–1938

45 Wild, G. *et al.* (2009) Adaptation and the evolution of parasite virulence in a connected world. *Nature* 459, 983–986

46 Boots, M. and Mealor, M. (2007) Local interactions select for lower pathogen infectivity. *Science* 315, 1284–1286

47 Best, A. *et al.* (2011) Host resistance and coevolution in spatially structured populations. *Proc. Biol. Sci.* 278, 2216–2222

48 Loehle, C. (1995) Social barriers to pathogen transmission in wild animal populations. *Ecology* 76, 326–335

49 Croft, D.P. *et al.* (2011) Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies *Poecilia reticulata*. *Behav. Ecol. Sociobiol.* 65, 2219–2227

50 Johnson, C.R. and Seinen, I. (2002) Selection for restraint in competitive ability in spatial competition systems. *Proc. Biol. Sci.* 269, 655–663

51 Prado, F. and Kerr, B. (2008) The evolution of restraint in bacterial biofilms under nontransitive competition. *Evolution* 62, 538–548

52 Nahum, J.R. *et al.* (2011) Evolution of restraint in a structured rock-paper-scissors community. *Proc. Natl. Acad. Sci. U.S.A.* 108, 10831–10838

53 Kerr, B. *et al.* (2006) Local migration promotes competitive restraint in a host-pathogen 'tragedy of the commons'. *Nature* 442, 75–78

54 Doebeli, M. and Knowlton, N. (1998) The evolution of interspecific mutualisms. *Proc. Natl. Acad. Sci. U.S.A.* 95, 8676–8680

55 Yamamura, N. *et al.* (2004) Evolution of mutualism through spatial effects. *J. Theor. Biol.* 226, 421–428

56 Mack, K.M.L. (2012) Selective feedback between dispersal distance and the stability of mutualism. *Oikos* 121, 442–448

57 Dunne, J.A. *et al.* (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567

58 Albert, R. *et al.* (2000) Error and attack tolerance of complex networks. *Nature* 406, 378–382

59 Williams, R. and Lusseau, D. (2006) A killer whale social network is vulnerable to targeted removals. *Biol. Lett.* 2, 497–500

60 Manno, T.G. (2008) Social networking in the Columbian ground squirrel, *Spermophilus columbianus*. *Anim. Behav.* 75, 1221–1228

61 Kanngiesser, P. *et al.* (2011) Grooming network cohesion and the role of individuals in a captive chimpanzee group. *Am. J. Primatol.* 73, 758–767

62 Flack, J.C. *et al.* (2006) Policing stabilizes construction of social niches in primates. *Nature* 439, 426–429

63 Moore, C. and Newman, M.E.J. (2000) Epidemics and percolation in small-world networks. *Phys. Rev. E* 61, 5678–5682

64 Newman, M.E.J. (2002) Spread of epidemic disease on networks. *Phys. Rev. E* 66, 016128

65 Watts, D.J. and Strogatz, S.H. (1998) Collective dynamics of 'small-world' networks. *Nature* 393, 440–442

66 Otterstatter, M.C. and Thomson, J.D. (2007) Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia* 154, 411–421

67 Clobert, J. *et al.* (2001) *Dispersal*, Oxford University Press

68 Tschirren, B. *et al.* (2007) Maternal modulation of natal dispersal in a passerine bird: An adaptive strategy to cope with parasitism? *Am. Nat.* 169, 87–93

69 West, S.A. *et al.* (2002) Conflict and cooperation: cooperation and competition between relatives. *Science* 296, 72–75

70 Hoogland, J.L. (2013) Prairie dogs disperse when all close kin have disappeared. *Science* 339, 1205–1207

71 Pusey, A. and Wolf, M. (1996) Inbreeding avoidance in animals. *Trends Ecol. Evol.* 11, 201–206

72 Bekoff, M. (1977) Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am. Nat.* 111, 715–732

73 Blumstein, D.T. *et al.* (2009) A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. Biol. Sci.* 276, 3007–3012

74 Ekernas, L.S. and Cords, M. (2007) Social and environmental factors influencing natal dispersal in blue monkeys, *Cercopithecus mitis stuhlmanni*. *Anim. Behav.* 73, 1009–1020

75 Gerlach, G. (1998) Impact of social ties on dispersal, reproduction and dominance in feral house mice (*Mus musculus domesticus*). *Ethology* 104, 487–499

76 Godfrey, S.S. *et al.* (2009) Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behav. Ecol. Sociobiol.* 63, 1045–1056

77 Godfrey, S.S. *et al.* (2010) Social network structure and parasite infection patterns in a territorial reptile, the tuatara (*Sphenodon punctatus*). *Int. J. Parasitol.* 40, 1575–1585

78 Kolar, C.S. and Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16, 199–204

79 Aplin, L.M. *et al.* (2012) Social networks predict patch discovery in a wild population of songbirds. *Proc. Biol. Sci.* 279, 4199–4205

80 Pinter-Wollman, N. *et al.* (2009) The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proc. Biol. Sci.* 276, 1009–1014

81 Beyer, K. *et al.* (2010) Social network properties within a fish assemblage invaded by non-native sunbleak *Leucaspius delineatus*. *Ecol. Model.* 221, 2118–2122

82 Kanarek, A.R. and Webb, C.T. (2010) Allee effects, adaptive evolution, and invasion success. *Evol. Appl.* 3, 122–135

83 Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170

84 MacLeod, C.J. *et al.* (2010) Parasites lost: do invaders miss the boat or drown on arrival? *Ecol. Lett.* 13, 516–527

85 Keeling, M.J. (1999) The effects of local spatial structure on epidemiological invasions. *Proc. Biol. Sci.* 266, 859–867

86 Wilson, A.D.M. *et al.* (2013) Network position: a key component in the characterization of social personality types. *Behav. Ecol. Sociobiol.* 67, 163–173

87 Lea, A.J. *et al.* (2010) Heritable victimization and the benefits of agonistic relationships. *Proc. Natl. Acad. Sci. U.S.A.* 107, 21587–21592

88 Lusseau, D. *et al.* (2011) Formalising the multidimensional nature of social networks. *arXiv* http://arxiv.org/abs/1101.3735

89 Kurvers, R.H.J.M. *et al.* (2013) Contrasting context dependence of familiarity and kinship in animal social networks. *Anim. Behav.* 86, 993–1001

90 Newman, M.E.J. (2003) The structure and function of complex networks. *SIAM Rev.* 45, 167–256

91 Moody, J. and White, D.R. (2003) Structural cohesion and embeddedness: a hierarchical concept of social groups. *Am. Sociol. Rev.* 68, 103–127

92 Bascompte, J. (2010) Structure and dynamics of ecological networks. *Science* 329, 765–766

93 Thebault, E. and Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856

94 Davies, N.B. *et al.* (2012) *An Introduction to Behavioural Ecology*. (4th edn), Wiley-Blackwell

95 Lima, S.L. and Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* 11, 131–135

96 Sutherland, W.J. (1996) *From Individual Behaviour to Population Ecology*, Oxford University Press

97 Kühl, H.S. and Burghardt, T. (2013) Animal biometrics: quantifiying and detecting phenotypic appearance. *Trends Ecol. Evol.* 28, 432–441

98 Krause, J. *et al.* (2013) Reality mining of animal social systems. *Trends Ecol. Evol.* 28, 541–551

99 Holmberg, J. *et al.* (2009) Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. *Endanger. Spec. Res.* 7, 39–53

100 Mennill, D.J. *et al.* (2012) A novel digital telemetry system for tracking wild animals: a field test for studying mate choice in a lekking tropical bird. *Methods Ecol. Evol.* 3, 663–672