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Review

Social Information Links Individual Behavior to Population and Community Dynamics

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When individual animals make decisions, they routinely use information produced intentionally or unintentionally by other individuals. Despite its prevalence and established fitness consequences, the effects of such social information on ecological dynamics remain poorly understood. Here, we synthesize results from ecology, evolutionary biology, and animal behavior to show how the use of social information can profoundly influence the dynamics of populations and communities. We combine recent theoretical and empirical results and introduce simple population models to illustrate how social information use can drive positive density-dependent growth of populations and communities (Allee effects). Furthermore, social information can shift the nature and strength of species interactions, change the outcome of competition, and potentially increase extinction risk in harvested populations and communities.

What Is Social Information and How Could It Be Important to Ecology?

As they go about their daily lives, organisms continuously produce information, both actively through signals (e.g., **alarm calls** [1,2]; see Glossary) and passively through **cues** (e.g., the act of fleeing can warn others of danger, and metabolic excretions can inadvertently provide information on the presence and physiological state of an organism [2,3]). This plethora of visual, acoustic, tactile, olfactory, and gustatory information means that organisms live in environments rich with insights into the identity, state, and actions of individuals in their neighborhood. A given piece of **social information** remains relevant to receivers for a limited amount of time (e.g., information on an attacking predator may be useful only for an instant) [4]. However, because social information is continuously produced, making use of it can improve the ability of an individual to make decisions over the long term, for example, by extending, beyond its own sensory abilities, the range or resolution at which it is able to perceive and respond to environmental gradients [5] or threats [1]. Behavioral ecologists have long studied how social information shared among conspecifics can influence habitat selection and trophic interactions [6–8]. Animals often use social information to acquire resources (e.g., individuals or groups feeding in a location alert others to food) [2,9–14] and to detect and avoid predators [1,2,6,15–17].

Social transmission of information about resources or danger occurs within species, as in the iconic examples of single-species flocks of birds or schools of fish; however, social information is also often transmitted among nearby individuals of different and sometimes distantly related species [1,4,18] (Box 1). For over a decade, seminal review papers have highlighted the evolutionary and ecological mechanisms that underlie social information use, and how this widespread phenomenon can affect animal behavior [1–4,18]. From these works and subsequent publications discussed below, it is clear that social information, shared within or across species, can have profound effects on animal behaviors and, in turn, can directly affect individual fitness [9,19] (Figure 1). Despite this, population and community ecologists have

Highlights

Mounting evidence shows that social information drives animal behavior and fitness in various ecological contexts, including habitat selection, foraging, and predator avoidance. However, only recently have researchers begun to implicate social information in the dynamics of populations and communities.

By driving correlations in the behavior and space use of many individuals that share resources or threats, social information can cause positive density dependence in behaviors that underlie individual fitness. Consequently, social information can drive positive density dependence (i.e., Allee effects) in population growth rates and resultant critical population thresholds, potentially affecting the extinction risk of populations and communities.

Social information can also affect the nature, strength, and dynamics of species interactions, allowing even strong competitors to coexist through facilitation.

Recent studies suggest that social information, often produced or used asymmetrically among individuals or species, generally affects how populations and communities respond to environmental change and, thus, is critical to consider in resource management and conservation.

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Box 1. Social Information Sharing Among Foraging Scavengers

Scavengers provide one of the best-studied examples of animals that rely heavily on social information, with studies of information sharing in the context of social foraging and competitive interactions within and across species dating back over half a century [92,93]. Given their feeding strategies, scavengers, such as Old-World vultures that specialize on large ungulate carcasses, often stand to benefit considerably by using social information. First, costs of information sharing are minimized, since carcasses are typically too large and ephemeral to be monopolized by a single individual or even small groups. Second, individuals benefit by using social information to both find and handle resources. Carcasses are challenging to find, because their locations are typically unpredictable, lack environmental cues (e.g., via strong associations with landmarks), and are scattered across vast areas [94,95]. Also, consumption of carcasses on the ground, where mammalian predators roam, poses a risk for vultures, which have slow take-off speeds (especially with a fully loaded crop) and typically embed their heads within the carcass while eating. These conditions make group foraging beneficial (Figure I) [70]. Thus, most vulture species tend to be colonial and/or form loosely connected search networks [96], in which individuals use social information to enhance their food intake rates and reduce their risk of starvation from stochasticity in local resource availability [95,97]. Field experiments show strong evidence that social information from individuals moving to or feeding from a carcass causes conspecifics and heterospecifics to follow this behavior [70,98,99].

Empirical findings, together with models [21,95], emphasize both the importance of information sharing during social foraging for individual fitness and the negative consequences of diminishing population sizes for the growth and persistence of the population. Furthermore, investigation of dependencies among species, where one species acts as a scout that produces information used by individuals of another species (e.g., lappet-faced and African white-backed vultures [70], eagles and Gyps vultures [58] or avian and mammalian scavengers [100]) illustrate how changes in community structure (e.g., local extinctions) can impact the fate of community members. A positive feedback loop, in which decreasing densities reduce the ability of the remaining individuals to find and/or access resources, can explain frequent population collapses in this guild [14,21,100]. Overall, this integration of approaches (observational, experimental, and modeling) provides insight into the role of social information in driving correlated behaviors in scavenger communities, offering tools to mitigate the detrimental effects of environmental change on the populations and communities of these sanitation providers.

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Figure I. A Lappet-Faced Vulture Landing into a Mob of Several Other Lappet-Faced Vultures, many African White-Backed Vultures and A Marabou Stork, all Aggregated in the Vicinity of a Fresh Zebra Carcass (to the Right). Photo credit: Orr Spiegel.

typically neglected to formally consider that individuals, particularly those within a species or trophic guild, influence one another's behavior [18,20]. Here, we fill this gap by highlighting how the use of social information can substantially affect population and community dynamics.

What makes social information ecologically pertinent is that it not only affects individual behavior, but it can also induce strong correlations in the behaviors and space use of many individuals [21–24]. Thus, social information can drive a range of behaviors, from mild conspecific attraction with no subsequent parallel behaviors (i.e., simple aggregation in space), to the highly synchronized individual actions that underpin the collective motion of flocks, herds, and schools [25,26]. Even loose, ephemeral associations among individuals can involve strong behavioral correlations driven by social information. For example, Gil and Hein [24] showed that foraging coral reef fish in loose, mixed-species aggregations decide when to enter and exit

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Figure 1. Empirical Studies Demonstrating the Use of Social Information by Animals. These studies come from a range of ecological contexts and taxonomic groups, and include both intraspecific and interspecific case-studies. For instance, (A) insectivore bats (*Noctilio albiventris*) eavesdrop on one another while foraging [54]; (B) starlings (*Sturnus vulgaris*) use social information to harvest resources, avoid predators, and assess habitats [6,89]; (C) coral reef fish use the movements of conspecifics and heterospecifics as cues to avoid predators and increase feeding rates [24,83]. While usually beneficial, reliance on social information can be detrimental if followed leaders are misinformed; for instance (D) bison (*Bison bison*) have been led by misinformed individuals to foraging grounds with high mortality risk due to hunting by humans [40]. Photo credits Silke Voigt-Heucke (A), Oded Ovadia (B), Michael Gil (C), and Orr Spiegel (D).

Glossary

Cue: information produced incidentally by the presence or behavior of an organism but that nonetheless becomes publicly available for use by other organisms.

Information cascade: when social information spreads, often rapidly, among many individuals to drive collective behavior.

Keystone informant: species in a community that provide disproportionately more value to other species through the provision of greater amounts or higher quality of social information.

Positive density dependence: when population size has a positive effect on population growth rate (also known as an 'Allee effect'), a phenomenon that can result from various mechanisms, including (but not limited to) social information use. In some cases, positive density dependence can cause an unstable internal equilibrium, and if a population falls below a threshold size it will experience negative growth and can be prone to rapid collapse.

Signal: information produced by the behavior of an organism with the intention of transmitting information to one or more other organisms.

Social inertia: the resistance to change that a population or community can experience due to engrained behaviors that are at least partially reinforced by social information shared among members.

Social information: the signals and/or cues produced by the presence and/or behavior of an organism and that can be used by other organisms (within or across species).

highly productive but exposed foraging areas based on the entries and exits of other fish (Figure 1C). This coupling of foraging decisions makes the overall foraging rate on algae sensitive to the local density and behavior of fish. This work highlights what is potentially a broad implication: when animals use social information to make decisions, not only do their locations and behaviors become correlated, but so do their interactions with predators, resources, and competitors. Such correlations in trophic interactions contradict the standard assumption that pairwise species interactions occur independently of one another, an assumption that underpins most models ecologists use to study populations and communities [11,24]. Thus, it could be crucial to consider the demographic consequences that these correlations can have both for our general understanding of ecology and for the conservation and management of ecological systems.

The theory of positive density dependence (i.e., 'Allee effects' [27]) is a useful starting point from which to study the demographic implications of social information. This point was made by Schmidt *et al.* [23], who showed that eavesdropping on the reproductive performance of conspecifics can enhance breeding habitat selection and, consequently, population growth. When individuals gain reproductive benefits by using social information that increases in abundance or quality with the density of information-producing individuals [21,22,28–30], this

phenomenon can drive **positive density dependence** in the growth rate of a population [23,31,32]. Positive density dependence can also result from mechanisms that do not involve social information (e.g., mate limitation or habitat amelioration) [27,33,34] and these can occur alongside information-mediated mechanisms. Historically, ecologists have recognized that cohesive grouping with conspecifics (e.g., schools, herds, and flocks) can underlie positive density dependence, with social information as the implied mechanism [27,35]. However, as we discuss further below, neither the formation of cohesive groups nor the reliance on conspecifics is a prerequisite for social information to drive positive density dependence. The importance of relying on social information can be particularly pronounced in a human-altered world, where populations and communities are often reduced to low densities [27]. If individuals rely heavily on social information to make decisions that affect their survival or reproductive success, positive density dependence could be more common than ecologists have previously believed [27,33,35,36]. Here, we show that social information-mediated positive density dependence can readily extend beyond populations to communities, when information is shared across species. Positive density dependence can not only lead to rapid population growth, but can also create critical thresholds, below which the population or community is prone to sudden collapse [14,27,33,35]. The latter consequence arises because the loss of individuals is increasingly detrimental to the survival or reproductive rate of those that remain, a phenomenon that has been shown experimentally to cause collapse in laboratory-based yeast populations [37,38] (Figure 2). Despite its general absence from mainstream ecology and conservation biology, the use of social information could qualitatively affect the long-term dynamics of populations and communities, and how natural systems respond to environmental change.

Here, we build on several key reviews [1–4,18] to formalize and generalize ideas presented in recent theoretical (e.g., [23,32,39]) and empirical (e.g., [22,24,40]) papers. Our synthesis unifies
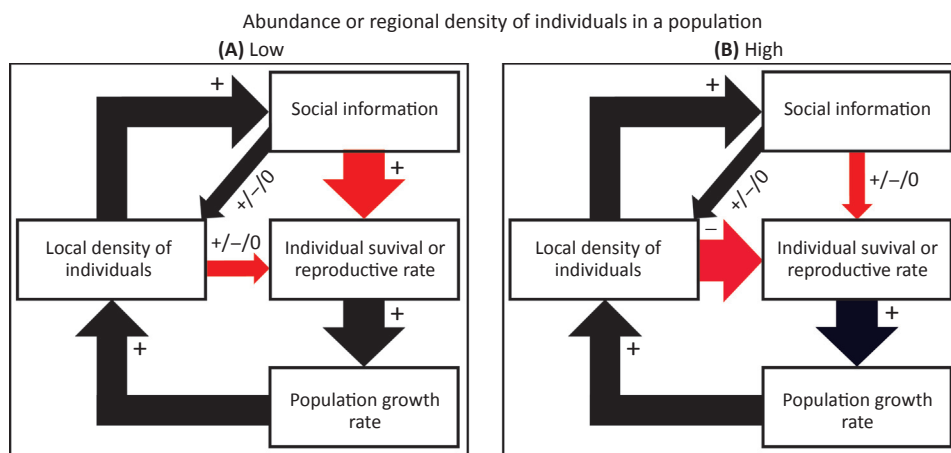
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Figure 2. The Density-Dependent Nature of Effects of Social Information on Animal Populations. When the abundance of a population or its regional density is low (A), we expect resource competition to be low (i.e., surplus resources regionally), such that the increased competition that occurs when local density increases can be outweighed by the benefits of increased access to social information. This can drive a positive feedback loop, whereby increased availability of social information facilitates population growth, which, in turn, increases the availability of social information. By contrast, when the abundance or regional density of a population is high (B), we expect competitive costs to outweigh the benefits of social information. Differences between panels are highlighted in red. The straight horizontal arrow represents non-information-mediated mechanisms by which local density affects individual fitness [27,42–44,90,91]. The diagonal arrow represents the effect of social information on local recruitment (e.g., conspecific attraction and/or repulsion) [26,41].

disparate bodies of literature in animal behavior, evolutionary ecology, population biology, and community ecology, and shows that social information can be important to a suite of fundamental concepts in ecology, including single-species population dynamics, interactions between a consumer and resource species, interactions among competitors, and ecological consequences of environmental change. We begin by outlining population-level effects, showing that social information-mediated Allee effects [23] can emerge in a range of systems and contexts. We then show how such Allee effects can extend to communities, illustrating how social information-mediated coexistence [39] arises when we quantitatively model a highly generalizable ecological context: competing species with a shared predator. We close with a discussion on heterogeneity in individual- and species-specific information production and use (examined mostly in avian systems [1,18]) and how these patterns can generally affect the dynamics of populations and communities and how ecological systems respond to environmental change.

How and When Does Social Information Use Affect Population Dynamics?

Social information has the potential to affect population dynamics in two primary ways: (i) by influencing the local density of individuals (e.g., via conspecific attraction); and (ii) by directly influencing the strength and direction (i.e., positive versus negative) of density dependence.

First, conspecific attraction induces spatial autocorrelation in the locations of individuals [26,41], and this phenomenon (or its foil, conspecific repulsion) can increase local population density in some places while decreasing it in others (e.g., social information can inform habitat selection by allowing individuals to assess habitat quality across heterogeneous landscapes). Local population density then affects demographic rates, such as reproduction and survivorship, where the typical focus is on the negative effect of population density on population growth rate, or 'negative density dependence' [27]. Mechanisms for negative density dependence include disease spread, competition for finite resources, and interference. Conversely, positive density dependence [27,33,35,36] can be driven not only by the information-mediated mechanisms mentioned above, but also through mechanisms not mediated by social information, such as reductions in abiotic stressors [42–44].

Second, social information can affect population dynamics when the utility of social information increases with population density [21,22,28–30], creating a positive feedback between population density and the reproductive success of individuals. As noted above, an individual that follows the behavior of others to locate resources or avoid predators can increase its own fitness, and, in doing so, increase its population size (i.e., the number of information-producing individuals that it and other conspecifics can follow in the future) [23,45,46]. For example, models reveal that higher densities of individuals can improve breeding success of eavesdropping conspecifics and, thus, increase the population growth rate at small population sizes [23,32]. Furthermore, individuals with different phenotypes can vary in traits that underlie the provision and use of social information. For instance, bolder barnacle geese produce more information, whereas shy individuals use this information more than others [47]. Thus, the density or spatial distribution of particularly informative individuals could have a disproportionate effect on population demographics [48,49], a concept we revisit in the section on community dynamics. Clearly, this kind of positive feedback has the potential to interact with negative density dependence in complex ways. To gain a qualitative understanding of how social information could manifest itself, we take a simplified view by considering cases where the benefits of social information outweigh competitive costs only at low population densities (i.e., when competition would be relatively low) (see Figure I in Box 2). Even over narrow density ranges, positive density dependence driven by social information can cause populations to experience critical thresholds, which, though believed to be common in nature, are often difficult to identify or predict [50–52] (see Figure I in Box 2).

Social information can further influence the relationship between population growth rate and density by altering the self-regulation of a population. Benefits of additional social information can saturate because of the inherent redundancy of repeated information concerning a stimulus or because information about a stimulus (e.g., a food patch) might be accurate for less time in crowded conditions [4,21,22,28,30] (Box 2). In certain cases, in lieu of resource competition, higher densities of individuals can undo or even counteract benefits of social information, by reducing the availability of useful information (e.g., through visual occlusion) or by increasing the frequency of energetically costly false alarms and attraction to depleted resources [53] (Box 2). Thus, diminishing returns of social information could reinforce population self-regulation and influence population carrying capacities classically attributed to competition, interference, or disease.

The Transmission of Social Information across Species Can Affect Community Dynamics

In addition to shaping individual populations, social information has the potential to influence interspecific interactions, community structure [18], and the dynamics of multispecies systems. Here, the same general mechanisms by which social information affects populations outlined in the preceding section can extend to communities of organisms, particularly those that have

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Box 2. Effects of Social Information on Population Dynamics

Here, we use a simple model to demonstrate how social information, in this case affecting predator evasion, can qualitatively and quantitatively affect the long-term dynamics of a population. Building on the classical logistic growth model, we follow population size N, with intrinsic per capita growth rate r and carrying capacity K. The population also experiences per capita mortality due to predation at a rate $B(N)$, such that its dynamics are (Equation I):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - B(N)N.$$ [I]

Without social information, the predation rate is independent of the population size, that is, $B(N) = p_c$, given constant predation rate p_c. With social information, a greater density of individuals can reduce per capita mortality due to predation, through the sharing of social information (e.g., via alarm calls or evasive movements) [1,2]. We use an exponentially decaying function to model a monotonic decline in mortality, where the effects of social information saturate as additional social information becomes less useful (e.g., due to redundancy) [4,21,22,28,30]. In this form, let b represent the per capita strength of the effect of social information, p_{soc} the maximum net effect of social information (on reducing mortality), and p_{min} the lowest mortality rate, which is reached when the net effect of social information has reached its maximum. The sum of p_{soc} and p_{min} represents base predation rate in the absence of social information, such that effective predation rate is (Equation II):

$$B(N) = p_{soc}e^{-bN} + p_{min}.$$ [II]

When $b = 0$ or $N = 0$ (i.e., information producers are minimized), this term collapses into $p_{soc} + p_{min}$, creating an equivalent predation term to p_c. As an alternative to this functional form, we also consider an inverse normal function to model cases in which reductions in per capita mortality due to social information manifest at low densities but are completely negated at higher densities (e.g., due to false alarms and/or occlusion of information) [53]. In this form, p_{max} sets the maximum predation rate, p_{soc} sets the maximum effect of social information in reducing $B(N)$ (as in Equation II), b controls the strength of the effect of social information and the (symmetric) strength of compensation, and N^* is the population size at which $B(N)$ is minimized by social information, such that the effective predation rate is (Equation III)

$$B(N) = p_{max} - p_{soc}e^{-(b[N-N^*])^2}.$$ [III]

Complete compensation for effects of social information is likely less common than cases of partial compensation (i.e., when benefits of social information are only partially negated at higher densities) [4,21,22,28,30]. Thus, the functional forms of Equations II and III represent opposing bounds on a continuum where most systems likely fall. In Figure I, we show that, regardless of its functional form (A), social information can alter quantitative dynamics, such as the realized carrying capacity [right sides of Figure IC and D, compared to Figure IB), and qualitative dynamics, such as the potential for alternative stable states and population persistence under high baseline predation relative to population growth (left sides of Figure IC and D, compared to Figure IB). This simple modeling framework could apply to various scenarios in which individuals help each other avoid predators through the provision of social information, which could be actively sought out [23] or, instead, incidentally acquired from surrounding conspecifics or heterospecifics.
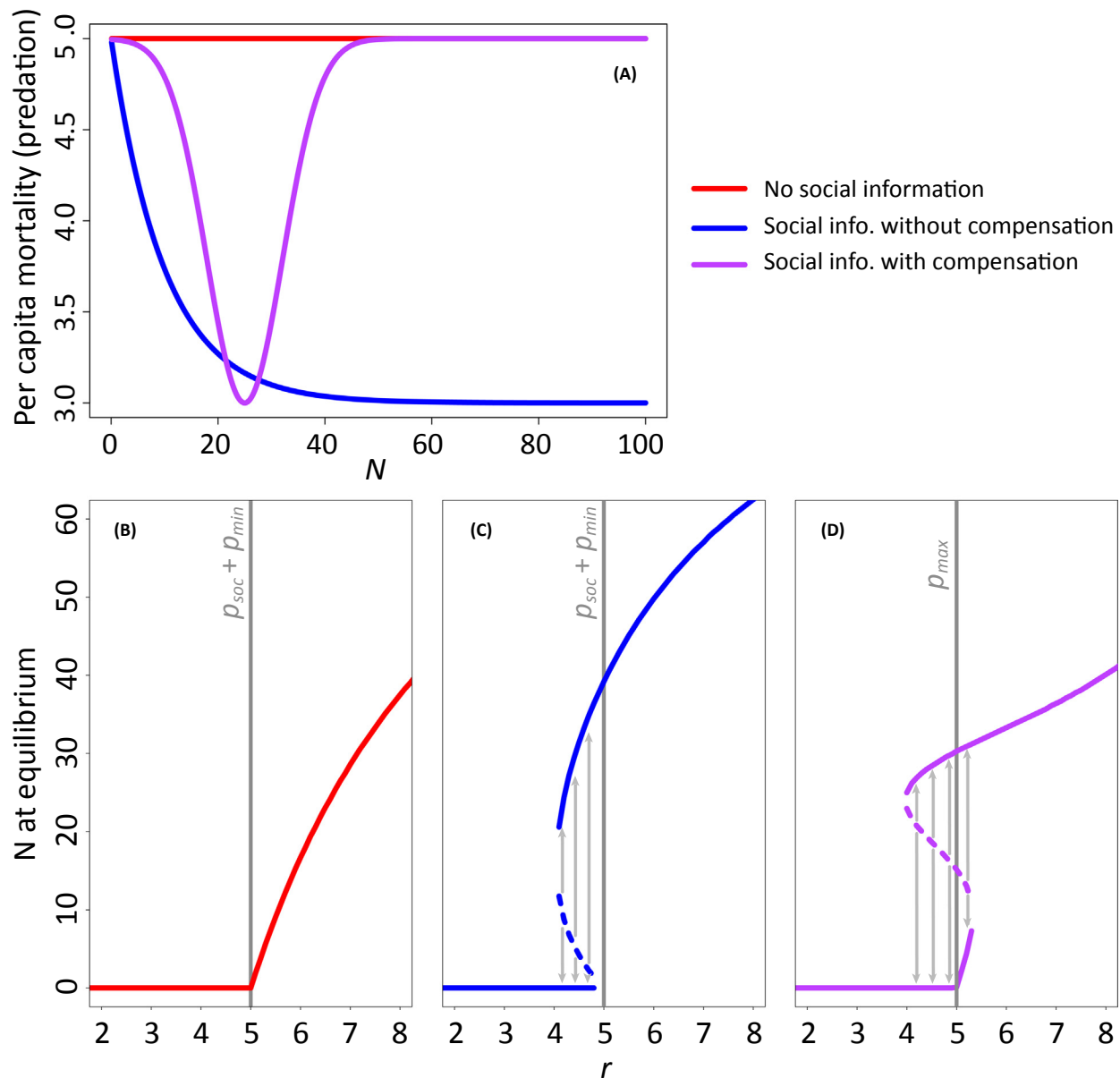
Figure I. How social information can affect population growth. Inclusion of social information effects on per capita mortality (A) expands, relative to the logistic model with predation (B), the conditions under which a population can persist and increases population size at equilibrium across a range of conditions (C,D). In particular, when per capita growth rate (r) exceeds maximum predation rate, denoted by the vertical grey lines ($r > p_{soc} + p_{min}$ for the model with social information [blue curve (C) Equation II in the box text] or $r > p_{max}$ for the model with social information and compensation [purple curve (D) Equation III in the box text]), social information increases the stable population size at equilibrium [right sides of (C,D)]. When maximum predation rate exceeds per capita growth rate ($r < p_{soc} + p_{min}$ or $r < p_{max}$; e.g., due to an environmental change, such as a species invasion that raises predation or a resource shortage or pathogen that lowers r), social information can give rise to alternative stable states. As a result, social information can prevent population collapse (shown on the left side of Figure IB) if population size does not fall below an unstable equilibrium that represents a critical threshold (denoted with the dashed lines on the left sides of Figure IC,D; *sensu* a 'strong Allee effect' [35]). For these calculations, we set $K = 100$, $p_{soc} = 2$, $p_{min} = 3$, $p_{max} = 5$, $N^* = 25$, and $b = 0$ for the 'no social information' model, $b = 0.1$ for both models with social information. It is the relative (not absolute) values of r and predation ($p_{soc} + p_{min}$, or p_{max}) that determine the dynamics.

shared resources or enemies [19]. For instance, echolocation-based foraging in bats produces an easily detectable cue that attracts conspecifics [54] and heterospecifics [55] to resource-rich areas (Figure 1A). Similarly, chemical and auditory signals drive heterospecific attraction in bees [56] and in ant-following birds [57], respectively, and visual cues drive heterospecific attraction in scavenger birds [58] (Box 1). The net benefit of using social information generated by heterospecifics depends on the type of information being shared and the degree of niche overlap between information producers and receivers [4,19,55,59].

Higher resource overlap among species results in both greater competition via resource depletion and greater benefits of using information about resources gleaned from these other species. This creates a tradeoff between competition and the quality of information about resources; thus, relative to conspecifics, heterospecifics can not only provide less information about relevant resources, but can also compete for resources less intensively and, similarly, can pose lower risks as disease vectors [4,19,59]. Work in bird communities suggests that this tradeoff drives an optimal degree of niche overlap for the interspecific exchange of social information about resources [60]. Interestingly, evolution and learning can fine-tune signals to increase the efficacy of useful information shared about resources. Field studies suggest that, when species overlap in foraging niche, simple conditioning results in seemingly complex heterospecific copying behavior [61]. As an example, signals produced among competing species in bird flocks converge on similar forms, as opposed to previously expected divergence into readily distinguishable forms [62]. By providing benefits such as enhanced predator avoidance or resource acquisition, the transmission and use of social information among species can provide a general mechanism for coexistence of species that would otherwise exclude one another via competition [39] (see Figure I in Box 3).

Social Information and the Facilitation–Exploitation Spectrum

Although the net benefits of using information produced by another species can be reduced by resource competition with that species, there are also situations where animals can gain strong benefits from interspecific sharing of social information with little competition. In such situations, one would expect mixed-species associations to be common. For example, by following the movements of other species within their mixed-species flocks, greater racket-tailed drongos benefit from the incidental flushing of their prey by species pursuing different prey [63]. More generally, when different resources or prey utilized by different species are correlated in time and space, or when resources or prey are plentiful, interspecific competition is nonexistent or weak. In these scenarios, social information that enhances predator avoidance can drive commensalism or mutualism, potentially enhancing the persistence of one or both interacting populations (Figure I in Box 3 III). Generally, the greater the degree to which heterospecifics share predators, the greater the usefulness of shared information about predators, which can, in turn, affect the likelihood of information use across species [19]. For example, among Australian passerines, whether one species responds to an alarm call by another species depends on the degree to which it shares enemies with that species (i.e., the relevance of the information) [64]. Interspecific social information can enhance predator avoidance through a variety of mechanisms, including flight by noncompeting heterospecifics providing early warning cues of imminent danger and alarm calls alerting eavesdropping heterospecifics to the presence of predators [1,2,18,65]. Furthermore, the saturating positive density dependence due to social information (Figure I in Box 2) prevents unstable population growth that can emerge from classic mutualism models [66,67] (Figure I in Box 3).

Just as species differ in competitive ability, species (or phenotypes within a population [49,68]) can differ in their abilities or roles as producers or users of information. For example, giraffes

Box 3. Effects of Social Information on Competing Populations with Shared Predators

Here, we expand upon the model presented by Equations I and II in Box 2 to demonstrate a simple modeling framework for measuring how social information can qualitatively affect the long-term dynamics of two competing populations. We follow population sizes N_i of each species i, where within-species population growth, density dependence, and baseline predation follow the same dynamics and notation as Equation I and II in Box 2, but these species compete with one another at a rate α_{ij}, which represents the per capita negative effect of the jth species on the ith species. Both species experience per capita mortality due to predation at a rate that is an exponentially decaying function (the two-species analog of Equation II in Box 2) of the densities of both conspecifics and heterospecifics, i.e., both conspecifics and heterospecifics share and use social information (e.g., alarm calls, evasive movements) to enhance predator avoidance [1,2]. In this form, b_{ii} represents the strengths of the effects conspecific social information and b_{ij} that of heterospecific social information, such that the dynamics of the ith species are (Equation I)

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \alpha_{ij} N_j}{K_i} \right) - N_i \left(p_{soc,i} e^{-\left(b_{ii}N_i + b_{ij}N_j\right)} + p_{min,i} \right). \qquad [\mathrm{I}].$$

In numerical solutions of Equation I for two species ($i \, \varepsilon \, [1,2]$), the inclusion of social information in either or both forms (via intraspecific or interspecific information sharing) can cause long-term outcomes that are qualitatively distinct from those that emerge when social information is absent. In Figure I, we provide a characteristic example of the general phenomenon that interspecific social information can drive coexistence of competing populations (Parejo *et al.* [39] used conceptual models to reach a similar conclusion). Interspecific social information can generally create one or more stable internal equilibria (causing coexistence for at least a subset of initial conditions) or enhance population sizes of coexisting species, unless effects of intraspecific social information and/or interspecific competition are sufficiently strong. In a follow-up paper, we will thoroughly examine the modeling framework presented here, including the relative importance of intraspecific and interspecific social information and competition in shaping species interactions and population dynamics.
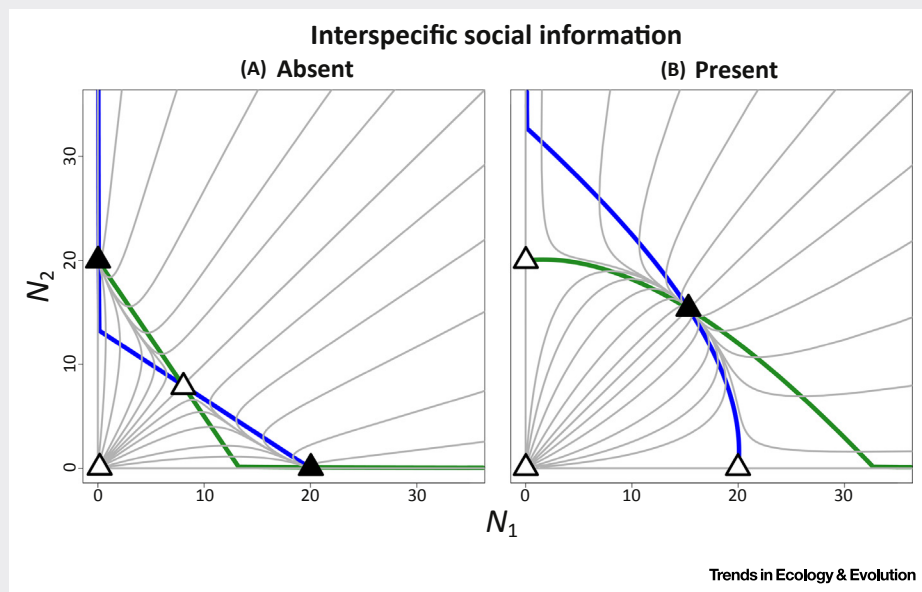

Interspecific social information

(A) Absent   **(B) Present**

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Figure I. Example Effect of Interspecific Social Information on the Persistence of Populations of Two Competing Prey Species. These plots feature nullclines that denote each of $\frac{dN_1}{dt} = 0$ (x-axis, blue lines) and $\frac{dN_2}{dt} = 0$ (y-axis, green lines) as a function of the other species. Grey lines show the trajectories populations take through time, starting from initial population sizes near the edges of the plotted area, and equilibria ($\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$) are denoted with triangles (open, locally unstable; closed, locally stable). Here, we start with a case where, when social information is absent (A), strong interspecific competition (> intraspecific competition) creates alternative stable states (stable edge equilibria, where only one species persists, with an unstable internal equilibrium) with competitive exclusion where the winner depends on initial conditions. However, when interspecific social information is present, strong interspecific competition can fail to drive competitive exclusion, and instead a stable internal equilibrium with coexistence can arise (B). For these calculations, we set $b_{12} = b_{21} = 0$ in A and $b_{12} = b_{21} = 0.04$ in B, while all other parameters were equal between panels: $r_1 = r_2 = 5$, $K_1 = K_2 = 100$, $p_{soc,1} = p_{soc,2} = 2$, $p_{min,1} = p_{min,2} = 3$, $\alpha_{12} = \alpha_{21} = 1.5$, and $b_{11} = b_{22} = 0$.

have higher vantage points that allow earlier detection of predators relative to cohabiting zebras, which, consequently, pay close attention to giraffes [69]. In mixed flocks, larger birds or scout species with better visual acuity extend the predator detection range of surrounding species with poorer sensory capacities [70]. Chickadees encode information about predator identity in alarm calls [71], making these calls particularly informative to multiple species of surrounding birds with shared predators [72]. In these cases, one particular species serves as a **keystone informant**. In avian systems, the removal of these species can cause the partial or complete dissolution of mixed-species flocks, resulting in reductions in habitat-specific feeding rates and body condition of a range of attendant species [68,73]. In addition, complementarity in the provision of useful information by different species (e.g., one species provides information about a specific resource or predator, while another species provides information about a different resource or predator) could generally promote mixed-species aggregations [70] and may produce positive effects of community density on the growth rate of the populations of involved species, even those in direct competition (Box 3). Species also differ in how they acquire social information: some actively seek out social information by positioning themselves near information-producing conspecifics [22,23] or heterospecifics [1,24,57]. However, social information can influence the behavior and potentially the demographics of wild animals even when it is acquired in a passive manner [e.g., as a result of the incidental locations of conspecifics (Box 2) or heterospecifics (Box 3) that detect a shared predator] [1,4,18,24].

Differences in the production of, or responses to, social information among species (or among phenotypes within a population) can result in asymmetries in the benefits of using social information [2,4,18,47]. For example, in mixed-species flocks compared with single-species flocks, foraging rates increased for the subordinate morphology of the Madagascar paradise flycatcher, *Terpsiphone mutate*, but failed to increase for the dominant (long-tailed) morphology, likely due to its lower maneuverability in the microhabitats to which it was led in mixed flocks [74]. Asymmetries in social information production and use can drive stable producer-scrounger dynamics [75], and information use without reciprocity can be parasitic, not only when information receivers are classically defined as parasitic (e.g., brood parasites using host vocalizations to locate nests), but also when information receivers are simply strong competitors for resources required by the information-producing species [2,76]. Moreover, some species (e.g., Amazonian flycatchers) can manipulate social information to facilitate kleptoparasitism: the stealing of foraging opportunities from competing flock members [77]. Thus, through multiple pathways, social information can affect the nature and strength of species interactions that structure communities and shape population dynamics.

Social Information and Ecology in A Changing World

If an environment changes, a common consequence of human activities, social information could reinforce behaviors that help populations avoid declines or collapse (e.g., see Figure I in Box 2), or, by contrast, reinforce behaviors that increase extinction risk under new conditions (e.g., perpetuating formerly adaptive but now maladaptive behaviors; *sensu* 'ecological traps' [78]). Computational models have shown that social information can improve the ability of groups of foragers to track resources that shift at small spatial scales and over relatively short, behavioral timescales [5,9,79] or between breeding seasons [32], but that large-scale or long-term environmental changes can eliminate these benefits or cause social information to become highly detrimental to populations [32,80,81]. For example, habitat fragmentation can reduce or cease migration in populations that rely on information from a small number of leaders, the leadership by which can fail to evolve in a fragmented landscape [80]. This effect could reduce population size and may not be easily undone with environmental restoration, due to strong hysteresis [80]. The notion that **social inertia** can limit behavioral plasticity and affect

responsiveness to environmental change has been demonstrated empirically for bison. In contrast to the previous theoretical example, leaders continued to function in a human-altered landscape, but to the detriment of the collective: a small number of individuals led migration to historically fruitful but now dangerous (human-dominated) foraging grounds, causing a population decline [40] (Figure 1D). As with social information originating from a small subset of leaders, social information provided by many individuals can drive detrimental responses to environmental change. For example, when migratory populations rely on information provided by a large collective, consumer removal (e.g., via harvesting) can (similar to the above example) reduce or prevent the ability of the entire population to reach an important destination [82]. Moreover, modeling selection on individual decision making in dynamic environments revealed that individuals that behave rationally based on all available information generally do not reach optimal decision-making. Instead, evolved individuals become overly reliant on social information, exhibiting delayed responses to environmental change, followed by rapid compensatory reactions that drive costly population volatility [81]. These dramatic reactions result from **information cascades**, in which individuals copy the behaviors of others that, themselves, are often simply copying the behaviors of others, as opposed to making decisions based on direct interactions with their environment.

In addition to the role of social information in mediating the responses of species to environmental change, environmental change itself can affect the efficacy of social information exchange. Perhaps most obviously, environmental change can reduce social information exchange by reducing the density or diversity of information producers. For example, social information use in intensively harvested consumer communities [24] could make associated ecosystems less stable and more susceptible to dramatic regime shifts if depletion brings functionally important populations near critical density thresholds. Environmental changes can also inhibit the delivery of sensory information, both directly to social information producers (e.g., due to inhibition of olfactory cues in degraded coral reefs, informant fish fail to identify and, thus, transmit information about the presence of predators [83]), or from producers to receivers (e.g., reduced visual detection of fleeing prey in turbid conditions [84] or muddled bird songs in noisy urban settings [85]).

A key, largely unexplored issue is the compensatory responses of organisms to disruptions to information-mediated interactions. For example, many animals have shifted their calling behavior to compensate for increased urban noise [85]. Overall, how environmental changes interact with the mode and use of social information to affect populations and communities will depend on heritable genetic variation and phenotypic plasticity in the ability of individuals to adjust their ability to produce, acquire, or rely on social information. In fact, new theoretical models suggest that alternating between social and asocial strategies across space or time sustains populations when either strategy alone will fail [86,87].

Concluding Remarks

In summary, social information provides a ubiquitous mechanism through which the behaviors of multiple individuals become correlated in space or time and, in doing so, can scale up to affect the dynamics of populations and communities. The use of social information could be a pervasive mechanism that determines the nature and strength of density dependence. Social information can give rise to positive density dependence that can cause critical thresholds that can accelerate population declines and drive sudden collapse (see Figure I in Box 2). Furthermore, the use of heterospecific social information can qualitatively affect species interactions, allowing stable coexistence when competitive exclusion or extinction would otherwise result (see Figure I in Box 3). Through various mechanisms, population and community-level effects of

Outstanding Questions

How pervasive is social information-mediated positive density dependence (i.e., Allee effects), and under what environmental contexts will social information give rise to critical population thresholds that can lead to sudden population collapse?

What biotic and abiotic environmental factors dictate the nature and strength of the effect of social information on population dynamics and species interactions?

How does social information, through its differential influence on various pairwise species interactions, affect interaction networks (e.g., food webs) and the structure and function of associated communities?

Can we predict whether social information will facilitate or inhibit an adaptive response to various forms of environmental change?

To what degree can the reliance of animals on social information adaptively change in a changing world, and how might this adaptive capacity be predictable based on species-specific characteristics, such as life history and phylogeny?

How important is it for social information to be explicitly considered in conservation and resource management (i.e., how can it influence the efficacy of different management approaches)?

social information could shift suddenly with environmental change and could have major consequences at the ecosystem scale [24,40].

Explicitly considering the effects of social information on the dynamics of populations and communities could qualitatively change predictions of ecological models, potentially allowing for better agreement between ecological theory and data, and more accurate insights for management into the many systems in which these effects can be strong. For example, by affecting expected thresholds necessary for population growth, social information could affect population viability analyses as well as reintroduction targets used by conservationists and resource managers. Although substantial logistical challenges remain in many systems, technological advances in the remote monitoring of individual behavior (e.g., via high-frequency tracking [88] or video-based surveillance [24]) are opening the door for new big data in the realm of field ecology, and this will be essential to properly characterize how social information spreads *in situ*. Future research should focus not only on further quantifying effects of social information on population and community dynamics, but also on measuring this in field conditions to understand the degree to which these effects depend on context (see Outstanding Questions). Ecological effects of social information could vary considerably with potentially interactive factors that include species, sensory modality, physiological state, and various environmental characteristics, each of which could raise or lower the amount, transmission, or value of social information. Generally, the potential for social information to affect the long-term persistence of populations, communities, and associated ecosystem processes and services appears to be high, yet remains a timely research frontier at the interface of ecology, evolutionary biology, animal behavior, and biological conservation.

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