

Social information use by competitors: Resolving the enigma of species coexistence in animals?

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Abstract. The competitive exclusion principle states that species limited by the same factors cannot share the same environment. Challenging this paradigm, empirical studies often report competitors' coexistence in natural communities, which has long puzzled evolutionary ecologists. Theoretical studies on animal communities have conferred a prime role to the negative effects of interactions in explaining coexistence, but largely neglected the potential positive side of interactions. Here, we propose that living close to a competitor could have beneficial aspects because competitors may provide fitness-enhancing social information, which under some circumstances may counter the negative effects of competition, thus promoting coexistence. We use conceptual models and discuss factors influencing social information use and their influence on the outcome of competitors' interaction in terms of coexistence probability. Finally, we discuss ecological and evolutionary implications of these processes and suggest exciting avenues for future research on animal communities.

Key words: community organization; competitive exclusion; niche overlap; positive interactions; social information.

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INTRODUCTION

Species coexistence has long puzzled evolutionary ecologists (Hutchinson 1961, Chesson 2000, Clark et al. 2007). It is evident, on the one hand, that a large number of species coexist in natural communities while, on the other hand, ecological theory predicts that coexistence of species sharing the same limiting factors would hardly be achieved because one of two competitors (Table 1) will always overcome the other, leading to local extinction or to evolutionary or behavioral changes of the subordinate species (Competitive exclusion principle: Gause 1934). To solve this

paradox stated by Hutchinson (1961) more than half a century ago, several mechanisms have been proposed (Wilson 1990, Holt 2001, Sommer and Worm 2002), all intending to explain how competitive exclusion may be prevented. These mechanisms could be categorized in three types: (1) the group suggesting that species avoid competition through resource partitioning by using slightly different niches (Table 1) and hence not being real competitors (MacArthur and Levins 1964, Warner and Chesson 1985). Alternatively, the disruption of competitive exclusion has been proposed to be based in either (2) external processes such as disturbance, predation, or

Table 1. Glossary of terms.

Term	Definition
Allee effect	Phenomenon characterized by a positive correlation between population size or density and the mean individual fitness of a population or species.
Biotic interactions	Relationships between two or more species in an ecosystem. They can be classified by the direction of their effects as positive, negative or neutral.
(a) Positive interactions	All nonconsumer interactions among two or more species that positively affect at least one of the two involved species. At an interspecific level, they may range from facilitation (at least one of the species is benefitted, and the other is either not affected (commensalism) or benefitted from the interaction (mutualism)) to antagonism (one species is benefitted while the other is harmed).
(b) Negative or agonistic interactions	Interactions that have a negative impact on at least one of the interacting species. Examples of negative interactions are predation, competition and parasitism.
Coexistence	The state of two or more species (or organisms) being found in the same place at the same time, such that none eliminates the other.
Competitors	Individuals that interact negatively by the use or defense of a limiting factor, which reduces availability of this limiting factor for other individuals. Limiting factors may be either resources or environmental conditions that limit the growth, abundance, or distribution of an organism or a population of organisms in an ecosystem (Smith & Smith, 2009). Therefore, competitors might compete for food, for nesting sites, for mates or for a enemy-free space.
Niche and niche overlaps	The niche of an organism consists of its role in the ecosystem (herbivore, carnivore, producer etc.), its tolerance limits (e.g., soil pH, humidity) and its requirements (shelter, nesting sites, ...) all varying through time. Niche overlaps occur when two organisms use the same resources or other environmental variables, that is when they share limiting factors.

herbivory removing individuals from the dominant species thus releasing competition (Neutral models, Hubbell 2001, Bell 2000); or (3) evolutionary trade-offs combined with environmental heterogeneity that may lead to interspecific differences in competitive ability for different resources, thus preventing competitive exclusion (Buss and Jackson 1979). Some of these mechanisms either lack empirical tests or received support only in some systems (Wilson 1990, Houle et al. 2006). Therefore, the paradox of species coexistence remains a conundrum in evolutionary ecology.

All above mechanisms explaining coexistence rely on the classical paradigm that negative interactions play the fundamental role in shaping communities (Schoener 1983). Only recently positive interactions (*sensu* Bertness and Callaway 1994, Table 1) have been considered to explain coexistence in intraguild mutualism (Crowley and Cox 2011) or between species from different trophic levels (i.e., noncompeting organisms) (Hunter and Aarssen 1988). Even in plants, where interaction studies focus on facilitative processes more frequently than in animals (Hunter and Aarssen 1988), studies have largely targeted on either competition or facilitation mechanisms but rarely on both (Lortie and Callaway 2009, but see Pugnaire and Luque 2001, Callaway et al. 2002), which is

challenging because competition and facilitation occur at the same time within a given system and combine to produce a net interaction effect (Callaway 2007). Indeed, theoretical work has suggested that considering facilitation, defined as nontrophic interactions between organisms that benefit at least one of the participants and does harm to neither, may help explaining key paradigms in ecology (Bruno et al. 2003). And currently, there is a growing trend to consider the effect of positive interactions when interpreting the structure of ecological communities (Bertness and Callaway 1994, Stachowicz 2001, Bruno et al. 2003, Crowley and Cox 2011, McIntire and Fajardo 2014).

Here, we hypothesize that the use of social information among competing species may help explaining their coexistence. Social information is extracted from interactions with, or observations of, other individuals (Wagner and Danchin 2010), and has been proposed as one of the possible, but not very common, facilitative mechanisms that may promote biodiversity (Parejo et al. 2005, McIntire and Fajardo 2014). Social information allows individuals to rapidly and inexpensively assess local resources and threats, and thus may enormously affect individual fitness (Seppänen et al. 2007, Schmidt et al. 2010). Our idea is that the positive effects of social information use in fitness-affecting decisions may, under some

circumstances, counter the negative effects of competition because competitors may provide reliable information on limiting factors, and thus favor competitors' coexistence. Notably, only competitors may provide valuable information on shared limiting factors (Parejo et al. 2005). Therefore, the simultaneous consideration of negative and positive effects of living close to competitors could help explaining species coexistence, and consequently the organization of animal communities.

In this article, we (1) illustrate how the balance between positive (through heterospecific social information use) and negative (through competitive processes) consequences of living close to competitors determines the situations in which their coexistence is possible, (2) outline factors influencing the value of social information and its influence on coexistence, and (3) discuss the ecological and evolutionary implications of these processes and most fruitful avenues for future research on natural communities. We primarily focus our discussion on animals; however, the proposed mechanism may work for any system where competing species could be affected by the facilitative aspects of social information, and we thus show a few examples with organisms others than animals.

SOCIAL INFORMATION AND ECOLOGICAL THEORY

Part of the background of the idea that the positive effect of social information use may favor coexistence had been to some extent explicitly included in studies on the use of social information in animal decision-making for several decades (see Elmberg et al. 1997, Forsman et al. 2002, Parejo et al. 2005, reviewed in Seppänen et al. 2007, reviewed in Valone 2007, Parejo et al. 2012, Loukola et al. 2013), but had never been formulated and developed as a mechanism to explain species coexistence within the framework of ecological theory. Previous reviews on the topic have considered facilitation as a biotic interaction providing benefits, but not prejudicing to participants (Bruno et al. 2003). That is, negative effects of facilitation, caused for instance by the local aggregation of individuals in sites with limited resources, have been generally ignored (but see Schoeb et al. 2014). In contrast, we propose here to consider both positive and

negative fitness consequences of using social information by competitors because it may be a highly dynamic process. Considering the negative aspects of facilitative mechanisms, such as social information use, changes the implications of these positive interactions, and constitutes the main difference between our proposal and that made by Bruno et al. (2003) of including facilitation into ecological theory.

SOCIAL INFORMATION USE

Social information can be inadvertently (including actions and consequences) or intentionally (signals) produced. Inadvertent social information results from facts that are unavoidably produced by organisms and may be detected and then used to improve decision-making by other organisms (Danchin et al. 2004). An example of inadvertent social information is mean local reproductive success of conspecifics, which may inform others about local habitat quality in terms of food, nest-sites, predation, and parasitism risk (Danchin and Wagner 1997). On the other hand, intentional information is that transmitted by signals, which are traits or behaviors which have been selected to transmit information (Danchin et al. 2004). A classic example is the alarm signals of birds, which are vocalizations produced by threatened individuals aiming to diminish own and relatives' risk of predation. Alarm signals, however, may also inadvertently inform on local predation risk to nonrelated conspecifics and heterospecifics sharing predators, which may improve their predator avoidance. In this sense, signals can also be considered inadvertent social information when their information is decoded by nonintended receivers (e.g., Parejo and Avilés 2007). In both cases, social information provides an estimate of environmental quality by revealing the outcome of activities and/or decisions of competitors and may, hence, affect individual fitness. There is, however, a difference between decisions and consequences as sources of social information (Seppänen et al. 2007). Others' decisions might be wrong potentially resulting in maladaptive informational cascades (Giraldeau et al. 2002). The consequences of these decisions, however, are more likely to accurately reveal the cause of the decision, i.e., the assessed resource and

hence they are often the preferred cues (Giraldeau et al. 2002, Seppänen et al. 2007).

Social information is usually cheaper to obtain than personal information because individuals do not need to explore to get the first while the costs and risks of exploration are implicit in gathering personal information (Laland 2004). To be profitable, social information must come from individuals limited by the same factors, which include conspecifics as well as heterospecifics with high niche overlap, i.e., competitors (Parejo et al. 2005, Seppänen et al. 2007). The information coming from conspecifics is more accurate than that from heterospecifics because conspecifics share more than individuals from different species. However, information extracted from heterospecifics may be more advantageous because due to the lower niche overlap, competition with heterospecifics is likely less intense than that with conspecifics. Furthermore, heterospecifics are more abundant than conspecifics and thus information from the formers may be more easily acquired (Seppänen et al. 2007). Here, we will only focus on information coming from heterospecifics as the aim was explaining species coexistence.

Examples of cues used as sources of heterospecific social information are: (1) *The presence of other organisms indicating preferred habitats and hence resource availability* (Monkkönen et al. 1990). For instance, the flat lizard *Platysaurus broadleyi* is attracted to birds feeding on figs, that are its preferred food (Whiting and Greef 1999), so that birds' presence is social information indicating to lizards the location of fig trees, (2) *the local success of heterospecifics, reflecting the potential of a site to affect fitness* (Nocera et al. 2006, Loukola et al. 2013). Loukola et al. (2013) demonstrated that the bad-informed migratory pied flycatcher (*Ficedula hypoleuca*) copied the nest-site preference of the well-informed resident great tit (*Parus major*) experimentally manipulated to show high fitness, and tended to reject sites where great tits exhibited low fitness; and (3) *alarm signals emitted by individuals of other species revealing local predation risk* (e.g., Parejo et al. 2012). For example, an experiment demonstrated that the migratory scops owl (*Otus scops*) chose breeding sites where little owls (*Athene noctua*) signaled low predation risk through their calls (Parejo et al. 2012).

Plants may also rely on social information from heterospecifics. For instance, wild tobacco plants with experimentally clipped sagebrush neighbors suffer less leaf herbivory than tobacco controls with unclipped neighbors as a consequence of induced resistance, which was mediated by the release of a volatile hormone by sagebrush plants (Karban and Maron 2002). Therefore, facilitative processes may occur because some plants may gain some benefit by being associated with others producing chemicals informing on herbivory risk. Finally, the use of social information is probably involved in bacteria communication (quorum sensing (Diggle et al. 2007)) through chemicals. Therefore, although our review primarily targets on animals, the facilitative aspects of social information could well affect other taxa.

SOCIAL INFORMATION USE AND COMPETITORS' COEXISTENCE: A FUNCTION OF NICHE OVERLAP

Niche overlap among competitors will determine whether coexistence is or not possible (Table 1, Fig. 1). This is so because niche overlapping will set the magnitude of the positive and negative fitness effects of being close to competitors. The competitive exclusion principle states that two species competing for the same resource cannot, temporal and spatially, coexist (Gause 1934) (Fig. 1). Thus, at low levels of niche overlap, coexistence would not involve a theoretical problem because individuals living together would not compete. However, high levels of niche overlap will induce high negative effects on coexistence through competition, but also high beneficial effects through social information use. The balance between negative and positive effects of this interaction will ultimately determine the conditions in which coexistence is possible. When species overlapping is high, all individuals within a community may act, at one time or another, as informers and informed and hence be benefactors and beneficiaries. In this scenario, social information use by competitors could be regarded as an example of mutualism because all actors get benefits in one moment or another, although individuals from the interacting species compete. Relationships among heterospecifics may be mutualistic as well when only one species provides information, whenever the informed

species provides the informant with some benefits different to information. For instance, gobies (*Cryptocentrus steinitzi*) emit warning signals to conspecifics under predation risk that are also useful for burrowing shrimps (*Alpheus* sp.). In return, burrowing shrimps construct burrows for both themselves and gobies (Karplus 1987). Also, coexistence can be favored at high levels of niche overlap, when one species is the informant and the other the informed one, but the informant species has no or low costs when sharing information, for instance when information is about threats (see below), which could lead to situations of commensalism. But, coexistence will be prevented whenever just one species provides information and this provision of information will bring a disadvantage, leading

to a situation of parasitism (Goodale et al. 2010) in which the informant species may try to avoid the gathering of information by the informed one (Seppänen et al. 2007). All these arguments together imply a change in the competitive exclusion principle, which could be paraphrased now as “competitors using the same niche may sometimes coexist if they provide valuable information to each other” (Fig. 1).

Including the benefits of using social information within the niche concept modifies expectations of the ecological place that a species may occupy. Hutchinson (1957) defined fundamental niche as the range of environmental conditions in which a species can live, and distinguished it from the realized niche, or the restricted physical space actually occupied by a species after considering negative interspecific interactions. Therefore, positive interspecific interactions were not included in these concepts (but see Bruno et al. 2003). We argue that by incorporating the use of social information provided by competitors, the realized niche may enlarge till the spatial limits imposed by the fundamental niche because the benefits of using social information may, in some circumstances, neutralize the negative effects of competition. Eckardt and Zuberbühler (2004) provided a nice example illustrating how the realized niche of one species may be enlarged by the use of heterospecific social information till being as large as the fundamental niche. Studying two forest monkeys, the Diana monkey (*Cercopithecus diana*), and the putty-nosed monkey (*Cercopithecus nictitans*), they discovered that despite the intense feeding competition they showed, both species formed near-permanent associations in which the nonresident putty-nosed monkey was maintained at very low densities by the best competitor Diana monkey. Experimental evidence showed that was the information provided by alarms calls of the subordinate putty-nosed monkey in response to a very dangerous monkey predator which led to tolerance among the two species (Eckardt and Zuberbühler 2004), apparently because for Diana monkeys’ information on threats might be more important than competition. In turn, the informant species are allowed by the informed one to make use of its preferred habitat. Thereby, it seems that by providing social information to a competitor, putty-nosed monkeys are allowed to enlarge their

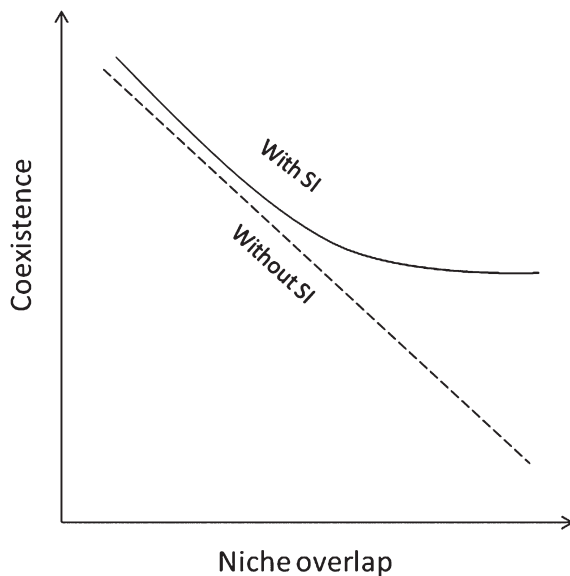


Fig. 1. Visualizing the level of species tolerance (coexistence) as a function of the niche overlap between interacting species. Coexistence is less likely to occur with increasing niche overlap as a consequence of increasing competition (discontinuous line). Adding social information use to the model (continuous line) coexistence is maintained at an intermediate level from medium to high levels of niche overlap because only species sharing resources and/or threats may provide valuable information. Indeed, the value of social information increases with overlapping needs and hence coexistence is more likely to be favored. SI: Social Information.

realized niche until the spatial range of their fundamental niche, which would be in the absence of competitors.

FACTORS AFFECTING THE VALUE OF SOCIAL INFORMATION USE FOR COEXISTENCE

Several factors may ultimately determine the situations in which competitors' coexistence is possible.

Symmetry of information use

Information use might be structured within communities of competitors provided that facilitative effects are not reciprocal for the two sides of the interaction. In such a case, the informers and informed individuals will have different benefits, and for the informed individuals, coexistence could be more likely achieved than for informers as the latter will only suffer the negative effects of competition and will not gain the benefits of social information. This is usually the case among migrant and resident birds because residents are better informed on breeding habitats than migrants due to a longer available time-window in which they can evaluate limiting factors (Monkkönen et al. 1990, Forsman et al. 2007). The highest level of asymmetry in the use of information happens when individuals parasitize information providers. Parasitism can result in benefactors developing defenses against information gathering by beneficiaries (Seppänen et al. 2007). Thus, informers are expected either to stop providing information or to avoid collectors to access information by hiding it or by keeping themselves far from information collectors, which would, in any case, prevent coexistence. Thereby, the migratory pied flycatcher uses the presence and density of resident tits (*Parus* sp.) to evaluate patch and nest site quality (Forsman et al. 2002). On the other hand, tits cover their eggs with hair before incubation, perhaps in an attempt to avoid other individuals to collect information about the presence and number of eggs (Seppänen et al. 2007), and they defend very aggressively nest-boxes against flycatchers if they meet in the nest box (Forsman et al. 2007). Hence, whenever competition is maintained constant, symmetric information use will favor coexistence more than asymmetric

(Fig. 2a). For instance, white-browed scrubwrens (*Sericornis frontalis*) share with superb fairywrens (*Malurus cyaneus*) feeding habits, alarm system, and predators. Unsurprisingly, they both respond to calls of the same and the other species and are able to coexist despite being competitors (Magrath et al. 2007).

Density of competitors

Population density is another important factor determining the outcome of the interaction among competitors. Fitness decreases with increasing competitors' density as a result of resource shortage (Rosenzweig 1981). The positive effect of using social information will be higher at moderate and high population densities than at low population densities when informative cues are often unavailable (Monkkönen et al. 1999, Fletcher 2006, Baude et al. 2011). When density of competitors is low, both low negative effect of competition and low positive effect of social information on fitness will be expected, so that the result may be slightly positive, neutral, or slightly negative as a function of the value of each effect in each situation (Fig. 2b). Nevertheless, at low density of competitors, coexistence should not be a problem because resources would be less likely limited. At high competitors' density, the strong negative impact of competition will outweigh the benefits of having social information available, hindering coexistence (Fig. 2b). Finally, at moderate population densities, both the beneficial effects of using social information and the negative effects of competition on fitness are likely to be moderate, which could lead to either neutral, negative, or more frequently positive effects on fitness (Forsman et al. 2002). This dynamic may help to understand positive density-dependent effects via Allee effect (Table 1). The increased fitness experienced by individuals in populations or communities at intermediate densities would be a consequence of the positive trade-off between competition costs and benefits of using social information. Indeed, some evidence suggests the existence of switches from negative to positive density-dependent effects in natural populations in response to changes in competitive pressure, either through changes in population densities (Ferrer and Penteriani 2008),

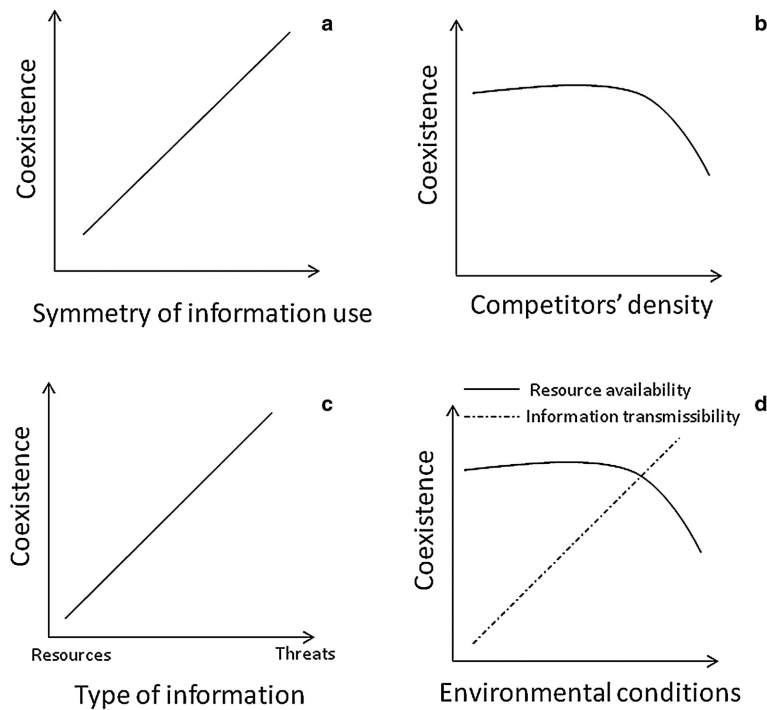


Fig. 2. Factors affecting species coexistence through their effects on the value of social information and on the level of competition. (a) Symmetry of information use: coexistence is more likely to occur when social information is useful for all interacting species (right part of the figure) than when one species provides information and the other uses it (left part of the figure). In this last scenario, the informant species gets no advantage and however, suffers the costs of competition by the aggregation with the other species. (b) Competitors' density: coexistence at low competitors' density is not a conceptual problem, but it is expected to decrease with increasing density of competitors. However, until a certain limiting density, at which competition imposes severe costs, social information provided by competitors may counter the negative effects of competition and coexistence may be favored. (c) Type of information: social information on threats is likely to favor coexistence more than social information on resources because predation is not likely to influence all members of a community as a scarcity of a resource may do. (d) Environmental conditions may affect both resource availability and conditions for information to be transmitted and gathered. Resource availability may determine the distribution of individuals and thus local density of competitors. Therefore, resource availability determined by environmental conditions will affect coexistence as density of competitors do (continuous line). On the other hand, coexistence will be favored more when environmental conditions favor more the transmission and gathering of information (discontinuous line).

or in environmental conditions (Bertness and Callaway 1994, Callaway and Walker 1997, Hart and Marshall 2013).

Type of information: Competitors informing on resources versus threats

Competitors may provide information about shared resources such as food and habitat, but also about shared threats such as predators and parasites. Individuals only compete for resources and not for threats. Thereby, social information

on threats is likely to favor coexistence more than social information on resources (Goodale et al. 2010) (Fig. 2c). Furthermore, local or temporal flocking in response to information on predation risk may be less harmful for informants than information on resources because in the former case, the association will help avoiding predation through a dilution effect. However, although competitors might benefit by sharing information on threats, they should overcome in some way the negative effects of

competition for limiting factors. For instance, in two sympatric competing birds, the migratory scops owl and the resident little owl, it was shown that scops owls were attracted to breed where the competitor little owl indicates low predation risk by its calls (Parejo et al. 2012). Costs of living close to competitors for little owls, that are the information providers, were not evident and must be low because niche overlap for this two species is mainly for nest sites and predators, and not much for prey. Alternatively, relationships among competitors of different species may be mutualistic when one of the species informs on threats and the other species provides the informer with some kind of benefit different to information as, for instance, a refuge to live (see above the example of gobies and shrimps, Karplus 1987, Goodale et al. 2010).

Environmental conditions

Environmental conditions may tip the balance to coexistence or avoidance (Bertness and Callaway 1994, Callaway and Walker 1997). In plants, positive interactions have been shown to increase with stress (Bertness and Callaway 1994) because when environmental conditions are severe, the density of competing plants is likely to decrease (following the ideal free distribution), leading to lower competition. In the same vein, the value of social information is likely to change with environmental conditions due to changes in population densities, being high at intermediate densities and maximum at high densities, and thus at intermediate and good environments (see above). Therefore, we would expect that the value of social information will exceed the negative effects of competition, favoring coexistence, mainly in moderated environments where competition must also be moderate and the number of info-providers will be enough to give valuable information on limiting factors (Fig. 2d). The environmental dependence of the result of the interaction among competitors, widely explored when addressing facilitation among plants, has been, however, neglected when studying positive interactions among animals. Indeed, aside from studies on heterospecific attraction among breeding birds suggesting that positive interactions may play an important role in shaping the

structure of northern bird communities (Elmberg et al. 1997, Monkkönen et al. 1997), studies addressing this topic are surprisingly scarce.

Furthermore, conditions may change the proportion of individuals of each population providing and using social information, and hence determine whether coexistence is possible. Within a population, there is individual variability in behavior that dictates how individuals will behave in certain situations. For instance, individuals may either personally assess the environment (producer tactic) or rely on the assessment made by others (scrounger tactic), and producing social information is usually mutually incompatible with using it (Giraldeau et al. 2002). Environmental conditions may determine whether producers or scroungers are dominant in the system, and hence define the level of tolerance among competitors. For instance, when resources are abundant, then the costs of searching are relatively low and thus there will be more producers than scroungers, which will benefit interspecific social information use based on a good sample of informers and hence coexistence. However, when search costs are high due to scarcity of resources, then the evolutionary stable strategy will shift toward a preponderance of scroungers, disfavoring coexistence.

Finally, environmental conditions may also determine the easiness of the information to be transmitted due to variation in visual, acoustic, and/or chemical transmissibility. These environmental conditions may also affect the value of social information and hence determine the trade-off between costs and benefits of competitors living together (Fig. 2d).

Interacting factors

All these factors may influence the value of social information and the intensity of competition either isolate or simultaneously, so that coexistence might be determined by complex interactions among them. For instance, the range of competitors' density over which coexistence is favored or disfavored depends on whether information use is symmetrical or asymmetrical (Fig. 3a). When the two interacting species are informers and informed at the same time, coexistence is likely to be easier than when one species acts as informant and the other as informed, and this will be so irrespective of the

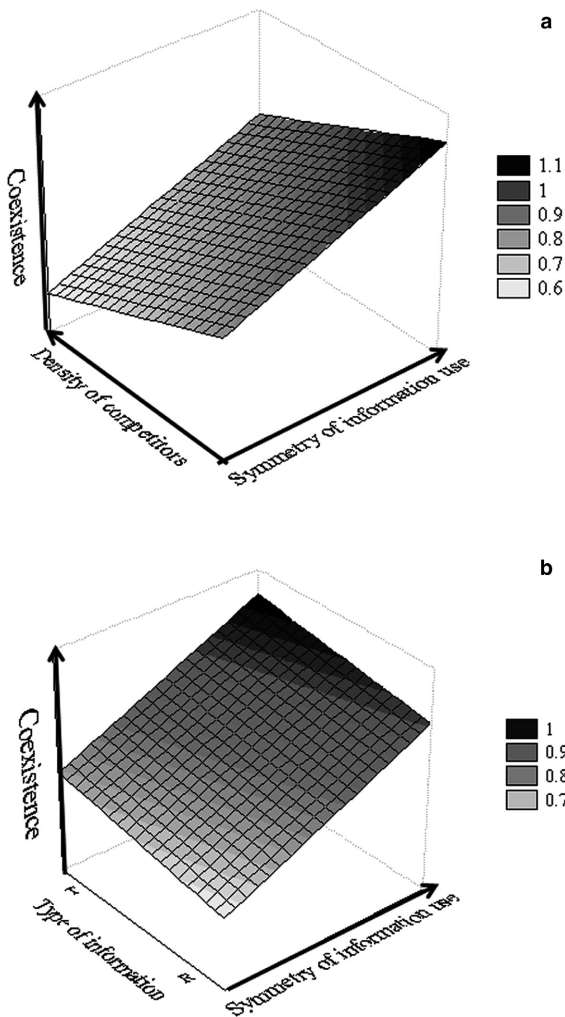


Fig. 3. Coexistence level including two factors each time potentially affecting the value of social information. (a) Density of competitors and symmetry of information use: Coexistence is more likely to occur when the use of social information is symmetrical within the community and population densities are low or intermediate. (b) Type of information and symmetry of information use: Coexistence is more favored under conditions of symmetrical social information use regarding threats.

density of competitors (Fig. 3a). Similarly, coexistence will probably be favored with the symmetry of information use more when individuals inform on threats than when they inform on resources (Fig. 3b) because individuals sharing only threats have less costs associated with competition. Also, abundant resources may

a facilitate coexistence at all levels of density of informers since resources increase the carrying capacity of ecosystems and thus reduce competition. Therefore, experimental approaches with different pairs of competitors (heterospecifics with different level of niche overlap) and manipulating the other factors (reciprocity of information use, density of competitors, the type of social information (on resources or on threats), and environmental conditions), either alone or in combination, would allow us to assess the net effects of competition and social information use on fitness and would provide empirical evidence on the changing value of positive and negative biotic interactions to structure communities of competitors.

b CONCLUSIONS

Our main aim was encouraging potential studies addressing how the benefits of using social information provided by competitors may help to explain the enigma of species coexistence. We argue that ecologists will gain deeper understanding about the structure of communities of competitors by considering the reciprocal nature of interactions due to the sharing of limiting factors. Both, the availability and value of social information and the intensity of competition, are likely to be affected by factors like the level of resource overlap among competitors, the symmetry of information use, density of competitors, type of limiting factor which social information tell on, and environmental conditions. These factors may influence the value of social information and the intensity of competition either isolate or simultaneously, so that these two dimensions determining coexistence might be a unimodal function of the affecting factors in interaction.

The proposed dynamic has evident ecological consequences because social information use may be playing more than just an anecdotal role in structuring animal communities through the compensation of competition. In evolutionary time, the use of social information in communities of competitors is likely to promote niche overlap, at least when environmental conditions are favorable. Summing up, we think that the inclusion of positive interactions among animals (and more generally the reciprocal nature

of interactions), specifically those resulting from the gathering and use of social information, in models of species tolerance is crucial to achieve a realistic view of community organization and that it may greatly help to reconcile differences between empirical and theoretical studies dealing with the intriguing questions of why and how competitors coexist.

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LITERATURE CITED

- Baude, M., E. Danchin, M. E. Mugabo, and I. Dajoz. 2011. Conspecifics as informers and competitors: an experimental study in foraging bumble-bees. *Proceedings of the Royal Society Series B* 278:2806–2813.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist* 113:223–234.
- Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. Springer, Dordrecht, The Netherlands.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Callaway, R. M., et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58:211–237.
- Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibañez, S. Ladeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. *Ecology Letters* 10:647–659.
- Crowley, P. H., and J. J. Cox. 2011. Intraguild mutualism. *Trends in Ecology and Evolution* 26:627–633.
- Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342–347.
- Danchin, E., L. A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491.
- Diggle, S. P., S. A. Crusz, and M. Camara. 2007. Quorum sensing. *Current Biology* 17:R907–R910.
- Eckardt, W., and K. Zuberbühler. 2004. Cooperation and competition in two forest monkeys. *Behavioral Ecology* 15:400–411.
- Elmberg, J., H. Poysa, K. Sjöberg, and P. Nummi. 1997. Interspecific interactions and co-existence in dabbling ducks: observations and an experiment. *Oecologia* 111:129–136.
- Ferrer, M., and V. Penteriani. 2008. Non-independence of demographic parameters: positive density-dependent fecundity in eagles. *Journal of Applied Ecology* 45:1453–1459.
- Fletcher, R. J. 2006. Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist* 168:207–219.
- Forsman, J. T., J. T. Seppänen, and M. Monkkönen. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society Series B* 269:1619–1623.
- Forsman, J. T., R. L. Thomson, and J. T. Seppänen. 2007. Mechanisms and fitness effects of interspecific information use between migrant and resident birds. *Behavioral Ecology* 18:888–894.
- Gause, G. F. 1934. *The struggle for existence*. The Williams and Wilkins Company, Baltimore, Maryland, USA.
- Giraldeau, L. A., T. J. Valone, and J. J. Templeton. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London Series B* 357:1559–1566.
- Goodale, E., G. Beauchamp, R. D. Magrath, J. C. Nieh, and G. D. Ruxton. 2010. Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution* 25:354–361.
- Hart, S. P., and D. J. Marshall. 2013. Environmental stress, facilitation, competition, and coexistence. *Ecology* 94:2719–2731.
- Holt, R. D. 2001. Species coexistence. *Encyclopedia of Biodiversity* 5:413–426.
- Houle, A., W. L. Vickery, and C. A. Chapman. 2006. Testing mechanisms of coexistence among two

- species of frugivorous primates. *Journal of Animal Ecology* 75:1034–1044.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Hunter, A. F., and L. W. Aarssen. 1988. Plants helping plants. *BioScience* 38:34–40.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Hutchinson, G. E. 1961. Paradox of plankton. *American Naturalist* 95:137–145.
- Karban, R., and J. Maron. 2002. The fitness consequences of interspecific eavesdropping between plants. *Ecology* 83:1209–1213.
- Karplus, I. 1987. The association between gobiid fishes and burrowing alpheid shrimps. *Oceanographic Marine Biology* 25:507–562.
- Laland, K. N. 2004. Social learning strategies. *Learning and Behaviour* 32:4–14.
- Lortie, C. J., and R. M. Callaway. 2009. David and Goliath: comparative use of facilitation and competition studies in the plant ecology literature. *Web Ecology* 9:54–57.
- Loukola, O. J., J. T. Seppänen, I. Krams, S. S. Torvinen, and J. T. Forsman. 2013. Observed fitness may affect niche overlap in competing species via selective social information use. *American Naturalist* 182:474–483.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the USA* 51:1207–1210.
- Magrath, R. D., B. J. Pitcher, and J. L. Gardner. 2007. A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology* 18:944–951.
- McIntire, E. J. B., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist* 201:403–416.
- Monkkönen, M., P. Helle, and K. Soppela. 1990. Numerical and behavioral-responses of migrant passerines to experimental manipulation of resident tits (*Parus spp*) - Heterospecific attraction in Northern breeding bird communities. *Oecologia* 85:218–225.
- Monkkönen, M., P. Helle, G. J. Niemi, and K. Montgomery. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Canadian Journal of Zoology* 75:2077–2083.
- Monkkönen, M., R. Hardling, J. T. Forsman, and J. Tuomi. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. *Evolutionary Ecology* 13:91–104.
- Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society of London Series B* 273:349–355.
- Parejo, D., and J. M. Avilés. 2007. Do avian brood parasites eavesdrop on heterospecific sexual signals revealing host quality? A review of the evidence. *Animal Cognition* 10:81–88.
- Parejo, D., E. Danchin, and J. M. Avilés. 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behavioral Ecology* 16:96–105.
- Parejo, D., J. M. Avilés, and J. Rodríguez. 2012. Alarm calls modulate the spatial structure of a breeding owl community. *Proceedings of the Royal Society of London Series B* 279:2135–2141.
- Pugnaire, F. I., and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93:42–49.
- Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology* 62:327–335.
- Schmidt, K. A., S. R. X. Dall, and J. A. Van Gils. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* 119:304–316.
- Schoeb, C., I. Prieto, C. Armas, and F. I. Pugnaire. 2014. Consequences of facilitation: one plant's benefit is another plant's cost. *Functional Ecology* 28:500–508.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.
- Seppänen, J. T., J. T. Forsman, M. Monkkönen, and R. L. Thomson. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* 88:1622–1633.
- Smith, T. M., and R. L. Smith. 2009. *Elements of ecology*. 7th edition, Benjamin-Cummings, London, UK.
- Sommer, U., and B. Worm. 2002. *Competition and coexistence-Introduction*. Springer-Verlag, Berlin, Germany.
- Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51:235–246.
- Valone, T. J. 2007. From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology* 62:1–14.
- Wagner, R. H., and E. Danchin. 2010. A taxonomy of biological information. *Oikos* 119:203–209.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* 125:769–787.

Whiting, M. J., and J. M. Greef. 1999. Use of hetero-specific cues by the lizard *Platysaurus broadleyi* for food location. *Behavioral Ecology and Sociobiology* 45:420–423.

Wilson, J. B. 1990. Mechanisms of species coexistence: twelve explanations for Hutchinson's paradox of the plankton: evidence from New Zealand plant communities. *New Zealand Journal of Ecology* 13:17–42.