REVIEW

Mixed-species aggregations in arthropods

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Abstract This review offers the first synthesis of the research on mixed-species groupings of arthropods and highlights the behavioral and evolutionary questions raised by such behavior. Mixed-species groups are commonly found in mammals and birds. Such groups are also observed in a large range of arthropod taxa independent of their level of sociality. Several examples are presented to highlight the mechanisms underlying such groupings, particularly the evidence for phylogenetic proximity between members that promotes cross-species recognition. The advantages offered by such aggregates are described and discussed. These advantages can be attributed to the increase in group size and could be identical to those of nonmixed groupings, but competition–cooperation dynamics might also be involved, and such effects may differ between homo- and heterospecific groups. We discuss three extreme cases of interspecific recognition that are likely involved in mixed-species groups as vectors for cross-species aggregation: tolerance behavior between two social species, one-way mechanism in which one species is attractive to others and two-way mechanism of mutual attraction. As shown in this review, the study of mixed-species groups offers biologists an interesting way to explore the frontiers of cooperation–competition, including the process of sympatric speciation.

Key words collective behavior; complex system; cross-species recognition; self-organization; sociality

Background

Over the last 40 years, research into collective behavior has rapidly expanded. In a milestone book, Krause and Ruxton (2002) reviewed the concepts underlying group-living, and they focused their work on the mechanisms that govern the evolution and maintenance of animal groups in several species. In 2010, Sumpter reviewed how the mechanisms driving group behavior are intertwined with its functions and concluded that simple rules may generate impressive and complex systems, such as migrating flocks of starlings, schools of fish or wildebeest herds.

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In this context, the study of collective behavior has mainly focused on intraspecific phenomena (Stamps, 1988; Camazine *et al.*, 2001; Sumpter, 2010; Kivelä *et al.*, 2014), especially in arthropods (see the review by Jeanson *et al.*, 2012). A Scopus search with "social" as the keyword (literature published from 2006 to 2016, performed June 13, 2016) returned 5099 research articles: 53% were on arthropods. But a large majority of the research on arthropod sociality is focused on eusocial species, especially ants and bees (Wilson, 1971; Krause & Ruxton, 2002; Sumpter, 2010). They are the topic of 78% of the scientific publications related to insects (Costa & Fitzgerald, 2005), likely because they form impressive societies, build complex nest structures and account for more than half of the insect biomass (Wilson & Hölldobler, 2005). In comparison, the keyword "mixed-species" found only 168 documents (Scopus searching

from 2006 to 2016). Furthermore, only 8% were on arthropods while more than half (58%) were on vertebrates (see, e.g., the reviews by Stensland *et al.*, 2003 and Terborgh, 1990 or researches by Farine *et al.*, 2014a,b) and 34% were on other living organisms (microorganisms, fungi, echinoderms, etc.).

Some of the best-known cases of mixed-species arthropods societies can be found in eusocial species (Fielde, 1903; Errard, 1994; Vauchot *et al.*, 1996). A striking example involves *Harpagoxenus canadensis* (a slave-making ant) invading *Leptothorax muscorum* nests to capture brood and rear them as slave workers (Stuart & Alloway, 1983). During this process, both species can be found working and living together in the nest, but after some time, *H. canadensis* appropriates the brood of the other species to restock its own colony. This temporary association challenges the conventional definition of an interspecific aggregation and highlights the unstable balance between different species that share the same ecological niche. Other examples of social parasitism in ants can be found in Huang and Dornhaus (2008). Nevertheless, true interspecific aggregations and cooperation are more often found in species with low levels of sociality (e.g., gregarious or communal; see the classification of sociality in Wilson, 1971), and these mixed groups can result from different behaviors and more-or-less complex interactions between species. This review attempts to assemble a comprehensive inventory of mixed-species arthropod groups through the perspective of collective behavior.

Definitions

First, it is important to draw a distinction between temporary groupings of individuals (groups that only form for mating or feeding) from gregariousness. This review focuses on mixed-species aggregations, that is, groups in which members of different species actively aggregate and remain together regardless of environmental heterogeneity or reproductive attraction (Fig. 1). Several other terms are used in the literature for groups composed of individuals of different species including heterospecific, interspecific, mixed-species, multispecies or polyspecific, so for the sake of clarity, the term mixed-species will be used throughout this review and can refer to closely related species, species from different taxa or species from different orders (Stensland *et al.*, 2003). Furthermore, two distinct notions can be used to characterize animal species that form groups (monospecific or mixed): social-tolerance and gregariousness. Tolerance is passive, and the underlying hypothesis is that *"a species' social tolerance (that) has evolved to fit its optimal population density*

and optimal population structure" (Barrows, 2011). This implies that individuals do not use aggregation vectors (mechanical, visual, and chemical channels), thus aggregates result from the attraction of individuals to the same environmental stimulus (Hamner & Schneider, 1986). In contrast, gregariousness is defined by Vulinec (1990) as *"the tendency of an animal to aggregate with others such that the animals are in contact with one another, or are nearly so, and that the distribution of the animals in the local environment is extremely patchy."* When considering this definition, it is important to include the idea of interattraction, which permits animals to create and maintain groups, and such interattraction can be direct or indirect (stigmergy, e.g., ground marking with chemicals). An efficient way to create mixed-species groups is to communicate with similar signals or to recognize the signals of other species. We named these signals as aggregation vectors and we will use this term throughout the text. In addition, the qualitative term "extremely patchy" used by Vulinec (1990) also needs to be moderated; indeed, depending of the characteristics of the interactions, the spatial distribution of gregarious populations can, in some cases, be weakly patchy (Dambach & Goehlen, 1999).

Types of mixed-species groupings

Mixed-species aggregations have been reported in various arthropods from aphids to butterflies and woodlice to ants (Costa, 2006) (Fig. 1), and they have been observed in terrestrial, aquatic/marine, and flying arthropods (Table 1). These groups can be composed of juveniles, adults, or, in most cases, both stages. Several kinds of mixed-species aggregations can be found: those observed in one stage (adults or juveniles), both stages, seasonally or artificially. Mixed-species groups composed of one or both stages can be frequently or occasionally observed in the wild.

A frequently reported example of larvae-only aggregation is that which occurs in necrophagous Diptera larvae (maggots; Fig. 1A). These species are very often found in mixed-species groupings on carrion. Adult females do not exhibit intra- or interspecific social behavior but lay their egg-batches in the same area on decaying tissue. This gathering may be due to the deposition of an aggregation pheromone during oviposition, as suggested in Rivers *et al.* (2011). However, Brodie *et al.* (2014) recently observed that eggs clustering is promoted by attractive semiochemicals produced by carrion flies while regurgitating and feeding on carrion. Gravid and nongravid individuals can detect such attractants, which rejects the idea of aggregations being mediated by oviposition pheromones. Whatever its form (tactile, chemical

Fig. 1 Examples of mixed-species groups. (A) Large mixed-species group of necrophagous Diptera larvae (*Chrysomya albiceps* [dark maggots] and *C. marginalis* [light maggots]). Species segregation is observed due to the specific thermal preferences of the larvae (used with permission—© Cameron Richards). (B) A mixed-species group of treehoppers composed of adults and nymphs (white) of *Membracis elevata* (black adults with a white spot on their back) and *M. dorsata* (adults without a white spot) found in Ecuador (used with permission—© Robert Oelman). (C) Lady beetles (*Harmonia axyridis*) and the spotted cucumber beetle (*Diabrotica undecimpunctata*) on grass (used with permission—© Nash Turley). (D) A large mixed-species group of woodlice composed of three species (*Armadillidium vulgare* (gray circle), *Oniscus asellus* (white circle) and *Porcellio scaber* (black circle); creative commons—Dave Ingram).

or visual), the eggs aggregation promotes the initial grouping of several species at the same place. This gathering is later reinforced and maintained by the active aggregation behavior of the larvae (Boulay *et al.*, 2013, 2016). However, as soon as larvae reach the prepupal stage, they leave the corpse and become strongly selfish for the rest of their lives.

Gatherings can also occur due to stochastic phenomena (i.e., by chance) (Briones-Fourzán *et al.*, 2008) or because one species is exceptionally present (Ayres *et al.*, 2001). A different degree of territoriality can also promote mixed-species groups (Grinsted *et al.*, 2012). Such a case has been reported for two lobster species, *Panulirus guttatus* and *P. argus* (Table 1). These two species occasionally share the same shelters without competition (Lozano-Álvarez *et al.*, 2007); *P. guttatus* tends to climb along the walls while *P. argus* occupies the floor. Each species uses the shelter space differently, which

promotes coexistence, and the aggregation allows *P. argus* to share the alarm odours of *P. guttatus*, enhancing protection against predators. Briones-Fourzán *et al.* (2008) suggested that such rarely observed mixed-species groups could be chemically mediated, but no evidence has been found. Some mixed-species groups also appear at a specific time each year. Ladybeetles, or ladybugs, form large, mixed-species aggregations inside buildings during winter (Simpson & Welborn, 1975; Lee 1980), and by forming such groups, they limit heat loss and reduce their mortality (Copp, 1983).

Finally, some artificial groups have only been observed under laboratory conditions. Some of them have been created from highly social species, such as ants or termites, while others gathered gregarious species (Table 1). Hodge and Storfer-Isser (1997) create artificial mixed-species spider clusters by provisioning the group with sufficient food until the adult instar was reached. Such an

Table 1 Known examples of mixed-species groups in different arthropod taxa. The pairwise divergence time was obtained using the website timetree.org (estimated time).

Taxon	Species	Pairwise divergence time (million years ago)	Life stage	Benefits	Underlying mechanisms	Nonsocial, one- or two-way recognition	References
Ants	*Manica rubida, Formica selysi*	111	Adults & juveniles	???	???	Two-way	Fielde, 1903; Errard, 1994; Vienne *et al.*, 1995
	Azteca constructor, A. xanthacrona	Same taxa	Adults & juveniles	↑ Production of workers, better reproductive success	Pleometrotic (2 queens)	Two-way	Choe & Crespi, 1997; Passera & Aron, 2005
Aphids	*Callipterinella calliptera, Betulaphis brevipilosa, Euceraphis betulae*	Same taxa	Adults & juveniles	↑ Production of honeydew, protection from predators (alarm pheromone recognition?)	Aggregation pheromone?	???	Hajek & Dahlsten, 1986
Bug	*Macrolophus pygmaeus, Nesidiocoris tenuis*	N/A	Adults	???	???	???	Moreno-Ripoll *et al.*, 2012
Butterflies	*Malacosoma disstria, M. americanum, Utetheisa* sp.	Same taxa	Adults & juveniles	Chemical protection, cannibalistic behavior avoidance, fitness (male pheromone production)	Trail-following abilities	Two-way	Fitzgerald & Edgerly, 1979; Bogner, 1996
Carrion flies	*Calliphoridae* spp., *Sarcophagidae* spp., *Muscidae* spp.	55	Adults & juveniles	Protection from predators, salivary enzymes sharing, heat generation, water loss limitation, ↑ survival rate	Shared oviposition sites, larval signal, heat, thigmotactism	Two-way	Ives, 1991; Reis *et al.*, 1999; Woodcock *et al.*, 2002; Gunn & Bird, 2011; Boulay *et al.*, 2013, 2016
Chrysomelids	*Phratora vitellinae, Plagiodera versicolora*	Same taxa	Juveniles	Protection from predators	Chemical cues	Nonsocial	Pasteels & Gregoire, 1984
Cockroaches	*Nauphoeta cinera, Leucophaea maderae*	105	Adults	???	Chemical cues	Two-way	Everaerts *et al.*, 1997

(to be continued)

Table 1 Continue.

Taxon	Species	Pairwise divergence time (million years ago)	Life stage	Benefits	Underlying mechanisms	Nonsocial, one- or two-way recognition	References
Collembola	*Orchesella cincta, O. villosa, Tomocerus minor*	284	Adults	???	Chemical cues	One-way	Verhoef *et al.*, 1977
Crabs	*Pagurus bernhardus, P. prideauxi*	Same taxa	Adults & juveniles	???	???	???	Meadows & Mitchell, 1973
Crustaceans	*Calappa calappa, Pachygrapsus planifrons, Lysiosquillina maculata, L. sulcata, Raoulserenea* sp., *Stenopus hispidus, Panulirus penicillatus*	356	Juveniles	Habitat selection	Chemical cues, visual cues	Two-way	Lecchini *et al.*, 2010
	Panulirus guttatus, P. argus	Same taxa	Adults	Recognition of alarm odours, shelter sharing	Chemical cues	Nonsocial	Lozano-Álvarez & Briones-Fourzán, 2001; Lozano-Álvarez *et al.*, 2007; Briones-Fourzán *et al.*, 2008
	Alonella, Ceriodaphnia, Chydorus, Megafenestra, Pleuroxus	Same taxa	Adults	Protection against predators	Similar behavior or pheromones emitted by *Scapholeberis?*	???	Kotov, 2000
Dermaptera	*Euborellia moresta, Forficula auricularia, F. decipiens, F. pubescens*	190	Adults & juveniles	Protection from predators	Chemical cues	Two-way?	Sauphanor & Sureau, 1993
Fleas	40 species listed by Stanko *et al.*, 2002	Same taxa	Adults & juveniles	Suppression of host immune system	Reduction of the size of the resource	Nonsocial	Krasnov *et al.*, 2005, 2006

(to be continued)

Table 1 Continue.

Taxon	Species	Pairwise divergence time (million years ago)	Life stage	Benefits	Underlying mechanisms	Nonsocial, one- or two-way recognition	References
Fruit flies	*Drosophila* sp.	Same taxa	Adults & juveniles	Limit fungal growth	Chemical cues, egg-batches, nonrandom distribution of oviposition sites	Two-way	Jaenike & James, 1991; Wertheim, 2005; Wertheim *et al.*, 2006
Lady beetles	*Hippodamia convergens, H. tredecimpunctata, Hypera postica*	239	Adults	↓ Mortality during winter, protection from predators and/or parasitoids?	Presence of aphid prey, environmental stimuli (T°, wind), chemical cues	Two-way	Copp, 1983; Honek *et al.*, 2007; Lee, 1980; Simpson & Welborn, 1975
Locusts	*Locusta migratoria migratorioides, Schistocerca gregaria*	81	Juveniles	Protection from predators	Chemical cues	Two-way	Niassy *et al.*, 1999; Uvarov, 1977
Mites	*Eotetranychus* sp., *Tetranychus urticae*	Same taxa	Juveniles	↑ Fertility, ↑ silk production, ↑ survival rate	Deposition of faeces, Intraguild predation, chemical cues, silk attraction (sericophily)	Nonsocial	Le Goff, 2011; Slone, 1999
Nitidulid beetles	*Carpophilus dimidiatus, C. freemani, C. mutilatus, C. antiquus, C. marginellus, C. humeralis*	Same taxa	Adults	???	Chemical cues	One-way	Bartelt *et al.*, 1993, 1995
Scorpions	*Buthotus judaicus, Compsobuthus werneri judaicus, Leiurus quinquestriatus*	Same taxa	Adults	???	Depends on season, specialization of scorpions for different prey, low aggressiveness	Nonsocial	Warburg, 2000

(to be continued)

Table 1 Continue.

Taxon	Species	Pairwise divergence time (million years ago)	Life stage	Benefits	Underlying mechanisms	Nonsocial, one- or two-way recognition	References
Spiders	*Hypochilus thorelli, Achaearanea tepidariorum*	308	Adults & juveniles	Web-building, website selection	Chemical cues, vibrational cues, silk attraction (sericophily)	One-way	Hodge & Storfer-Isser, 1997
	Serracutisoma proximum, S. spelaeum	Same taxa	Adults & juveniles	Protection against predators	Chemical cues?	Two-way	Chelini *et al.*, 2012
Stink bugs	*Nezara viridula, Chlorochroa ligata, C. sayi, Thyanta pallidovirens, Euschistus conspersus, Eurydema* sp.	Same taxa	Juveniles	Protection against desiccation, developmental acceleration, ↓ predation mortality rates, better adherence to substrate	Tactile cues, chemical cues	Two-way	Fucarino *et al.*, 2004; Ishiwatari, 1976
Tenebrionid flour beetles	*Tribolium castaneum, T. confusum, T. freeman*	Same taxa	Adults	Attraction of sexual partners	Chemical cues	Two-way	Arnaud *et al.*, 2002; Ryan & O'Ceallachain, 1976
Termites	*Reticulitermes santonensis, R. lucifugus grassei*	Same taxa	Adults & juveniles	???	Chemical cues	Two-way	Vauchot *et al.*, 1996
Ticks	*Haemaphysalis longicornis, H. megaspinosa*	Same taxa	Juveniles	↓ Water loss	Chemical cues	Nonsocial	Sonenshine, 1985; Tsunoda, 2007
Treehoppers	*Aconophora nitida, A. mexicana*	Same taxa	Juveniles	Protection from predators, maternal care	Stochastic phenomenon or shared oviposition sites by females	Nonsocial	Olmstead & Wood, 1990; Wood, 1979

(to be continued)

Table 1 Continue.

Taxon	Species	Pairwise divergence time (million years ago)	Life stage	Benefits	Underlying mechanisms	Nonsocial, one- or two-way recognition	References
Triatomine bugs	*Triatoma infestans, T. sordida, T. guasayana, Panstrongylus megistus*	36	Adults & juveniles	Better exploitation of protected places	Chemical cues, faeces	Two-way	Lorenzo & Lazzari, 1998; Mota & Lorenzo, 2012
Trilobites	*Ampyx, Asaphellus*	N/A	Adults	???	???	???	Chatterton & Fortey, 2008
Whirligig beetles	*Gyrinidae* sp.	Same taxa	Adults	Predator avoidance, ↑ defensive secretion	Mechanical stimuli (water waves), chemical cues (pygidial secretion?), visual cues, orientation to neighbours	Two-way	Heinrich & Vogt, 1980; Vulinec & Miller, 1989
Woodlice	*Porcellio scaber, Armadillidium vulgare, Oniscus asellus*	161	Adults	Protection from desiccation, ↑ production of faeces (secondary food source)	Tactile cues, chemical cues	Two-way	Broly et al., 2016; Yoder et al., 2005

N/A: not available; ↑: increase; ↓: decrease; ???: unknown.

environmental condition and sericophily enabled sociality (aggregation) that does not exist in the wild, highlighting a possible effect of habituation/collective breeding. By experimentally modifying the environmental conditions, Hodge and Storfer-Isser (1997) forced a species that naturally aggregates with conspecifics to assemble with heterospecifics. Similar results were observed by Warburg (2000) in scorpions.

Such artificial groups are interesting models to explore the minimum parameters needed to form mixed-species groups. These studies also highlight the crucial role of early social experience on the ontogeny of kin and nestmate recognition, and their results support the fact that mixed-species groups are often composed of phylogenetically related species (Table 1.) Phylogenetic proximity likely facilitates cross-species recognition, which is a necessary mechanism to initiate and maintain mixed-species groups. Such proximity also allows the use of similar aggregation signals (visual, chemical, etc.), thus facilitating the formation of mixed-species groups.

Aggregation vectors and cross-species recognition

To aggregate, stabilize, shape, reassemble or even split a group, gregarious species need efficient aggregation vectors (Lachmann *et al.*, 2000), which, in arthropods, are often based on the perception of chemical cues (e.g., cuticular hydrocarbons) as occurs in cockroaches (Amé *et al.*, 2004) or ladybirds (Durieux *et al.*, 2012). Despite being mostly unknown, interspecific chemical signals are also likely involved in mixed-species groups as vectors for cross-species aggregation. Wertheim (2005) highlighted 3 types of interspecific chemical interactions with (i) natural enemies (predator–prey relationship), (ii) microbial organisms (e.g., the relation between *Drosophila antiqua* aggregation pheromones and microbial or fungal growth), and (iii) the ecological community. For this last interaction, Wertheim (2005) highlights that the composition of the aggregation pheromones of some closely related species are similar, and this chemical similarity promotes mixed-species groups. A well-known example of information sharing in mixed-species groups are cockroaches. Everaerts *et al.* (1997) reared two species of cockroaches together, namely, *Nauphoeta cinera* and *Leucophaea maderae*, in the same environment. Under natural conditions, the chemical profiles of these two cockroach species are highly species-specific and used for intraspecific aggregations (Lihoreau & Rivault, 2009), but when reared together, these two species established interspecific chemical communication. Far from expressing simple

tolerance behavior (Fig. 2), the individuals aggregated together, increasing the size of the group (Everaerts *et al.*, 1997). The authors also observed a change in the chemical profile of the hydrocarbons in both species. Everaerts *et al.* (1997) hypothesized that this hydrocarbon transfer occurred during the frequent physical contact among group members, and such contact typically occurs in the early life stages of individuals and persists over time. In 1994, Errard reared *Manica rubida* and *Formica selysi*, two ant species, in a mixed-species colony for different time periods and observed a gradual increase in the tolerance behavior of both species. Furthermore, the individual hydrocarbon profiles of both species gradually acquired the chemical profile of the mixed colony (Errard, 1994). The establishment of the social group occurred in the early adult stage and was maintained through imprinting of mixed-colony cuticular hydrocarbons. Interestingly, the individuals reared in the mixed-species colony were not attacked by allospecific individuals reared with nonmixed nestmates, suggesting that there is a minimal quantity of allospecific hydrocarbon compounds necessary for allospecific recognition (Errard, 1994). Vienne *et al.* (1995) also observed a similarity between hydrocarbon profiles in two ant species. One species being more tactile (dominant species) than the other, the touching between individuals created a common cuticular hydrocarbons profile in this mixed-species. While apparently simple, this process is favored by relative phylogenetic proximity among species and long cumulative physical contact to allow chemical transfer.

The cross-species recognition is an essential mechanism to create and maintain mixed-species aggregation. The phylogenetic proximity between species can favor such recognition and so promote the formation of mixed-species groups. Related species often share some communication abilities (chemical, tactile, or visual channels) that facilitate the communication between individuals. Regarding mixed-species groups listed in the Table 1, more than a half (55%) are composed by species of the same taxa and 10% are composed by relative related species (pairwise divergence time inferior to 100 Mya (million years ago) based on timetree.org). This observation support the hypothesis that the phylogenetic proximity facilitates the formation of mixed-species. But such proximity is not a necessary condition for individuals to form mixed groups. Indeed, 30% of mixed-species groups listed are composed by species with a pairwise divergence time superior to 100 Mya (for 5% of listed examples there is no data; timetree.org). Even if the phylogenetic proximity between species favor the formation of mixed-species groups, it may also increase the competition as these species likely share close ecological niches (Kaplan
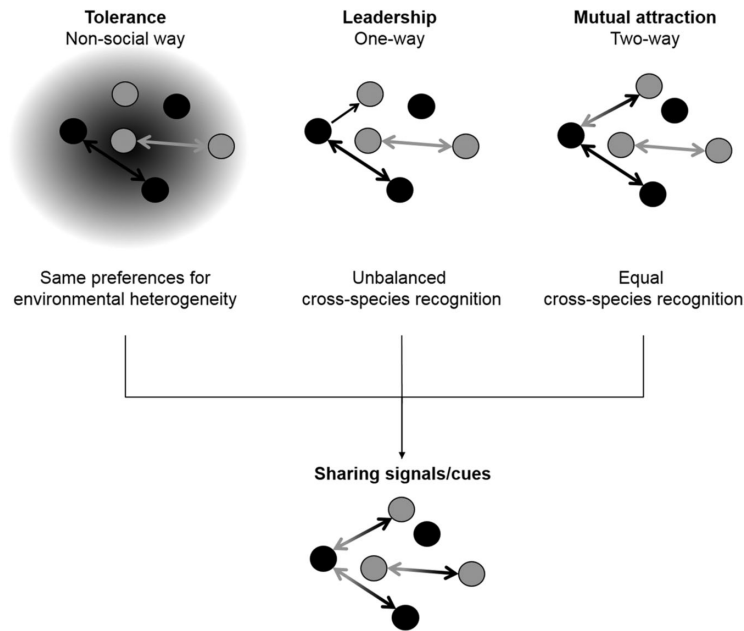
Fig. 2 Three extreme cases of interactions between species conducive to the formation of mixed-species groups. The nonsocial way is described as a gathering of tolerant species with the same preferences for environmental heterogeneity. In the one-way mechanism, one species is a tolerant leader or nucleus that forms the mixed-species group. The two-way mechanism is a mutual attraction of both species that is conducive to the formation of the group. Sharing signals/cues conduct to the maintenance of the mixed-species group in time. Arrows represent the detection of aggregation signals.

& Denno, 2007). A trade-off seems to stand out between the formation and the maintain of mixed-species groups. Such balance is between the sharing of communications ways (increased by the phylogenetic proximity) and the risk of competition (decreased by a relative divergence of the species).

Three extreme cases of interactions can maintain members in mixed-species groups (Fig. 2). First, tolerant species can create a group that is only based on having the same preferences (e.g., shaded places), which is a nonsocial way to aggregate; such a case has been reported in crustaceans (Lozano-Álvarez *et al.*, 2007). Cross-species recognition can also be a 1-way mechanism, meaning that one species is a tolerant leader or nuclear species that forms the mixed-species group (Srinivasan *et al.*, 2010). Palestrini *et al.* (1998) observed such unbalanced interspecific attraction in dung beetles. However, in many cases, cross-species recognition is a two-way mechanism (see examples in Table 1), which requires two species to be able to recognize each other and exchange information; such a case has been suggested by Boulay *et al.* (2016) to explain frequent mixed-species groups of Calliphoridae larvae. This kind of mechanism relies on equal exchange between species, meaning that both intraspecific and interspecific attractions are similar.

However, the one-way and two-way mechanisms represent two extreme situations, and various experimental results strongly suggest that two-way recognition is not always symmetrical; more often, individuals prefer conspecifics. Accordingly, Broly *et al.* (2016) suggested a stronger intraspecific attraction relative to interspecific attraction in woodlice groupings. In contrast, Meadows and Mitchell (1973) observed a stronger aggregation of *Pagurus bernhardus* with crabs of another species. However, although beneficial in the context of aggregation, identical aggregation vectors can also be a constraint due to overlapping signals. These signals can hamper responders from distinguishing intraspecific members, which may explain the advantage of an asymmetric mechanism.

Arthropods can also use physical communication to form mixed-species groups. Hodge and Storfer-Isser (1997) described the utilization of chemical and vibrational cues as aggregation vectors in two web-building spiders, *Hypochilus thorelli* and *Achaearanea tepidariorum*. This aggregation is supported by an interspecific attraction to silk that favours the formation and maintenance of the group in one website. As shown by Devigne *et al.* (2011) and Broly *et al.* (2012) in woodlice, thigmotactism (i.e., the search for contact) can also be a strong aggregation vector. The use of simple visual

cues can also lead to the formation of mixed-species groups. Mizell *et al.* (2012) described evidence of visual responses to conspecific and heterospecific congeners in two leafhopper species, *Homalodisca vitripennis* and *Oncometopia nigricans*. The authors used visual baits, such as leafhopper cadavers or coloured models, to attract individuals, and found that the presence of conspecifics or heterospecific congeners was used by the two species to estimate the quality of the host plant. The authors also observed that *H. vitripennis* responded to cadavers of the similarly sized heterospecific *O. nigricans*. Using this information, the leafhoppers chose to rejoin the heterospecific congeners on the same host plants. Similarly, Lecchini *et al.* (2010) showed that postlarval crustaceans preferentially used visual cues over chemical cues to detect heterospecific individuals and thus select their habitat. Indeed, individuals rely on the presence of heterospecific crustacean congeners to determine habitat quality, which could explain mixed-species aggregations.

Benefits

The notion of gregariousness often implies cooperation and/or competition, and these two phenomena are the most fundamental principles that drive the evolution of social structures. In 1931, Allee was the first to observe and to experimentally test for a positive relationship between a fitness component and population size or density (Stephens & Sutherland, 1999; Courchamp *et al.*, 2008). Indeed, aggregation offers direct benefits for group members and gathers reproductive individuals together, thereby facilitating reproduction. Based on this pioneering study, Odum (1953) named this relationship *the Allee principle*, which is more widely known as the "Allee effect." However, there are only a few empirical and theoretical studies of the consequences of the Allee effect for mixed-species animal groups (Courchamp *et al.*, 1999).

First, the benefits of aggregation can simply result from the number of individuals. Known examples of such benefits include protection against predators, protection against environmental constraints or foraging advantages (Parrish & Edelstein-Keshet, 1999; Riipi *et al.*, 2001; Weed, 2010). One of the most studied benefits of aggregation is protection against predators, which is commonly said to be one of the main advantages of aggregation (Evans & Schmidt, 1990; Vulinec, 1990). Predation risk is reduced by the presence of many individuals whose detection abilities are specific to their species (receptors increased). Cooperative defense (i.e., an increase in the number of predator detectors), also known as *the many eyes and ears theory*, is one of the few benefits that has

been studied in mixed-species groups. Indeed, this mechanism could be more efficient in a mixed-species group because each species contributes its specific predator detection abilities. In insects, Pasteels and Gregoire (1984) reported a defensive aggregation of two chrysomelid larvae, *Phratora vitellinae* and *Plagiodera versicolora*, on a *Salix* tree. These two species secrete a defensive substance against the female sawfly, *Tenthredo olivacea*, their common predator. According to the authors, the aggregation may be a social adaptation to efficiently repel enemies and increase the chance of survival. On the other side, the transmission of disease within aggregation is an important aspect that shouldn't be ignored (Wilson *et al.*, 2003). But in the case of mixed-species groups, such transmission could also be decreased, as has been suggested to occur in maggots (Rivers *et al.*, 2011; Wilson *et al.*, 2015).

The advantages of mixed-species groups can also be attributed to the direct increase in group size (just as in single-species aggregations); that is, individuals cooperate to reach an optimal group size so that each individual will gain direct benefits. When different species gather, even more individuals can be aggregated and more benefits can be gained. A striking example is provided by terrestrial crustaceous woodlice, for which desiccation is a major concern as they are very sensitive to water loss. In response to this environmental stress, aggregation has been shown to offer protection against drying (Broly *et al.*, 2014) (Fig. 1D). In this context, Hassall *et al.* (2005) also demonstrated that two species of woodlice, *Porcellio scaber* and *Armadillidium vulgare*, can clump together (see also Caubet & Richard, 2015). Consistent with the Allee effect, these authors found that at low densities, mixed-species groups promote population growth that results in positive fitness consequences (higher growth rates and survivorship of group members) (Hassall *et al.*, 2005). Furthermore, *A. vulgare* is more resistant to desiccation than *P. scaber* (Hassall *et al.*, 2010), and Broly *et al.* (2015) demonstrated that body shape explains the difference in the mass-specific water loss rates. As a likely consequence, *P. scaber* aggregates more than *A. vulgare* (Hassall *et al.*, 2005), and it can be supposed that *P. scaber* joins with *A. vulgare* to form a larger group that is better able to withstand low relative humidity and/or high ambient temperatures. For monospecific groups, *the selfish herd theory* postulates that individuals placed at the center of an aggregation reduce their risk of harm compared to conspecifics present at the vanguard (Parrish & Edelstein-Keshet, 1999). Such a mechanism holds for mixed-species groups, and may evenly be amplified by the different characteristics of the species.

Living together may also improve access to food. Hassall *et al.* (2005) hypothesized that mixed-species

woodlice aggregations provide individuals with an additional food resource because these species are detritivorous and feed on each other's feces. Another interesting example is provided by the larvae of carrion flies (Diptera: Calliphoridae) (Rivers *et al.*, 2011) (Fig. 1A), whose maggot masses can gather hundreds to thousands of individuals of several species and instars. These larvae secrete digestive enzymes and antibiotics, and their movements mechanically liquefy muscles to facilitate the assimilation of food (exodigestion). This benefit is likely a consequence of a simple numerical effect; if more individuals are present in a group (regardless of the species), more salivary enzymes are produced (Wilson *et al.*, 2015). Moreover, larvae secrete species-specific antibiotics (Rivers *et al.*, 2011) that decrease the number of pathogens on the carrion and thus increase larval survival. In this context, Ives (1991) quantified the strength of larval competition in carrion flies and demonstrated a reduction in interspecific competition relative to intraspecific competition through resource partitioning.

Thus, mixed-species can offer advantages that are not available to small monospecific groups. Furthermore, the addition of two or more species can yield different benefits than those observed in monospecific groups (e.g., different sensory abilities). However, while it may seem that the benefits of grouping are more or less equally shared when individuals belong to the same species, this assumption becomes questionable for groups composed of different species. In other words, one may ask if for the same group size, a monospecific group can be more effective than a mixed one. An initial response to this question is that the accumulation of the different abilities of the species in a mixed group can generate benefits that cannot be matched in the monospecific group. Such a phenomenon has been previously reported in mammals (Stensland *et al.*, 2003), and Roth and Willis (1960) suggest that it can also be true in arthropods. Through the association of the abilities of different species (cooperation), the benefits/deleterious effects ratio can be better compared to that observed in a monospecific group. Furthermore, species that form mixed societies mostly do not have the exact same ecological niche, which decreases the competition for food. All of this raises the question of benefit symmetry among group members. In social foraging groups, *the producer-scrounger game* is one of mathematical models used to describe the individual foraging strategies of group members (Giraldeau & Caraco, 2000). This model highlights the exploitation of a producer's findings (e.g., resource sites) by scroungers and predicts how foraging strategies change with food patch size. It also predicts how individuals can switch between the two strategies, scrounging or producing, until they reach an evolutionarily stable strategy (Giraldeau & Beauchamp, 1999). Such models have been used for many bird species (Giraldeau & Caraco, 2000; Sumpter, 2010) but, to our knowledge, only in non-mixed species groups. However, this model could be modified to describe the foraging strategies of mixed-species groups by adding parameters to quantify the different foraging abilities of each species. Such an upgraded model would be useful for predicting the ways in which species search and compete for resources in mixed groups.

Species competition

The question of competition is a key point in understanding mixed-species groupings. Surprisingly, even though mixed-species groups are interesting models for exploring the balance between collective benefits, species-specific benefits and competition within species and individuals, almost no experimental data can be found in the literature (Fig. 3).

The close proximity of competitors that occupy the same ecological niche decreases food availability or the accessibility of reproductive partners, so competition can emerge between members of mixed-species groups in habitats with insufficient food resources. However, Anne and Rasa (1989) suggest that competition decreases in mixed-species rather than single-species groups; individuals must compete for all of their resources in monospecific groups, while competition may be for only a single resource (food) in mixed-species groups (Anne & Rasa, 1989). Consistent with this idea, Reis *et al.* (1999) observed a higher survival rate in double-species groups composed of *Chrysomya putoria* and *Cochliomyia macellaria* when they increased the larval density of both species. However, they also showed that *C. macellaria* is an inferior competitor in the presence of *Ch. putoria*, as before coexistence depends on the condition that the cadaver size is not limiting. Thus, even if aggregation offers advantages, there may also be unbalanced relationships in mixed-species groups or even social parasitism, in which some species disproportionately benefit from the competitive abilities of another species. Moreover, the mechanical exclusion of one species by another may also occur, or the trade-offs between the species may change over time. At first, individuals of one species may gain from cooperating with those of another species to form a group, but once the group is formed and stable, species can mutually separate once their optimal group size is reached. If the two species have sufficiently different ecological niches, they can segregate but remain in contact (Figs. 1A & 3). This mechanism has been observed in two larval Diptera species, *Chrysomya albiceps* and *C. marginalis* (Villet
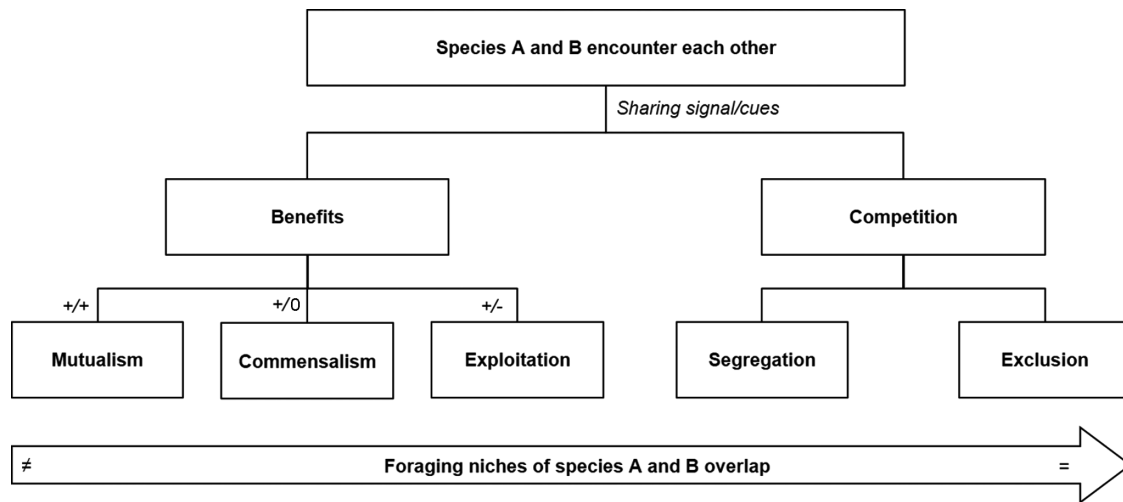
Fig. 3 Schematic overview of relationship between species in mixed-species groups. The overlap of ecological niches drives the interactions among species. Mutualism: a relationship between two species in which both benefit from the association. Commensalism: a relationship between two species in which one derives some benefit, while the other is unaffected. Exploitation: a relationship between two species in which one derives some benefit while the other is negatively affected. Segregation: a competitive relationship between two species that splits the group but the species remain in contact or close to each other. Exclusion: a competitive relationship between two species leading to the exclusion of one species from the area. The effects on the species can be (+) beneficial, (−) detrimental, or (0) neutral.

et al., 2010). These species grow faster at high temperatures, but each one has its own thermic preferendum. Due to their abilities to produce heat (larval-mass effect), they can aggregate together and increase local temperature. However, such aggregates split when mass-temperature start to exceed the tolerance of one species (Rivers *et al.*, 2011). Competition for access to food was observed in necrophagous larvae, which densely aggregate on carrion. Inside these larval masses, individuals try to reach the food located under the mass and thus crawl over each other in a movement described as "scramble competition" (Rivers *et al.*, 2011). However, Charabidze *et al.* (2011, 2013) highlighted that these masses are more structured than typically thought; according to the self-organization theory, a complex structure can emerge from larval foraging behavior, allowing them to feed more efficiently. More generally speaking, while the resource is not limiting, species can occupy a similar/identical ecological niche without experiencing the effects of competition, as in leaf-feeding aphids (Hajek & Dahlsten, 1986). However, many resources are restricted in quantity, time or space, which may contribute to restricting the ecological niches that are suitable for mixed-species groups.

Conclusion

Based on this review of the literature, mixed-species aggregations appear to be found in a wide range of arthropod taxa (Table 1). The phylogenetic proximity tends to favor the formation and the maintaining of such groups, likely due to similar scales (size, lifespan, displacement, etc.) and an easier communication between members. However, the degree to which the speciation process may be linked to the existence of stable mixed-species groups remains to be answered. Mixed-species groups do not seem to be restricted by the degree of sociality of the species; they have been observed in species ranging from gregarious to eusocial. Drawing on this, this review raises the question of the proximate and ultimate causes favoring such mixed-species groups, and one conclusion is the importance of the spatial distribution/specialization of the species. Obviously, natural mixed-species grouping is restricted to species of approximately the same size that at least partly share the same area during the same period of time. Species that form stable social groups are also more likely to accept individuals from another species. Furthermore, closely related species are likely to share similar aggregation cues (e.g., related chemical compounds) and detection abilities, which facilitates cross-species recognition and, probably, the formation of mixed-species groups. But theoretical models also show that the cues of both species do not need to perfectly overlap to produce mixed-species groups (Nicolis *et al.*, 2016). Furthermore, mixed-species groups can also be observed if the interattraction between species is less than the intraspecific attraction but greater than a critical value. The

similarity of the cues of the two species modulates the interattraction between them (Nicolis *et al.*, 2016).

Blends of chemical compounds (e.g., hydrocarbons) are the most common aggregation cues used by arthropods. Experiments on cross-species chemical recognition have been performed in only a restricted number of species, but they could provide an interesting starting point for understanding the mechanisms driving mixed-species aggregation dynamics, especially in the context of self-organization. Indeed, such aggregation dynamics result from a network of feedbacks, mainly the amplification of positive feedbacks resulting from interattraction, and this concept successfully explains how interactions between individuals can generate complex collective systems. Furthermore, self-organization is associated with the notion of emergence (a phenomenon is emergent when observers cannot predict its appearance based only on the knowledge of the behavior of the components of the system). From unicellular organisms to mammals, this theory has been used to describe collective phenomena and to explain how individuals can form, amplify, regulate or divide groups; many examples of emergent phenomena are described in Camazine *et al.* (2001). In the case of mixed groups, self-organized models predict different collective behaviors without the need to change the behavior of any individuals. Some generic parameters, such as resource availability (e.g., the carrying capacity) or the number of individuals involved, are the keys to shaping the aggregates. A simple but striking consequence is the possibility for species to segregate even in absence of agonistic behavior (Nicolis *et al.*, 2016).

From a purposive point of view, mixed-species groups likely provide similar benefits to members as intraspecific groups, a conclusion that was also drawn from mixed-species groups of mammals (Stensland *et al.*, 2003). These benefits essentially include enhancing protection against predators and shared foraging strategies (Table 1), and as shown by the examples in this review, mixed-species groups can be stable in time and mutually beneficial, especially if the species do not have the same ecological niche or if resources are not limiting. In such cases, the competition between species should play a secondary role, and both species can benefit from the aggregation and the resulting cooperation. However, interspecific competition can quickly direct the benefits disproportionately towards one species at the expense of the other. Experimental and theoretical results show that an increase in competition can lead to new patterns and a shift towards segregation (Leoncini & Rivault, 2005; Nicolis *et al.*, 2016). Accordingly, the study of mixed-species groups offers an interesting way to investigate the frontiers between cooperation and competition.

Compared to intraspecific groups, and especially eusocial species, our understanding of mixed-species groups of arthropods is at an early stage (see the review by Jeanson *et al.*, 2012), but most of the experimental designs used to study monospecific groups, such as the binary choice test, can be applying to the study of mixed-species groups (Leoncini & Rivault, 2005; Boulay *et al.*, 2016). Several marking techniques also exist to follow individuals, which can facilitate the monitoring of species during experiments (Hagler & Jackson, 2001), and such technical approaches provide a good working basis for further experimentation on mixed-species groups. Moreover, various theories, mathematical models and metrics have been developed in the context of aggregation and could be applied or adapted to mixed-species groups (for metrics, see Ives, 1991; Sauphanor & Sureau, 1993; Everaerts *et al.*, 1997 or Caubet & Richard, 2015; for models, see Deneubourg *et al.*, 1991 or Nicolis *et al.*, 2016). However, models of the cooperation–competition phenomenon still need to be established for mixed-species groups, but the required experimental data are currently lacking.

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Disclosure

The authors declare no competing interests.

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