
















Mixed company: a framework for understanding the composition and organization of mixed-species animal groups

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ABSTRACT

Mixed-species animal groups (MSGs) are widely acknowledged to increase predator avoidance and foraging efficiency, among other benefits, and thereby increase participants' fitness. Diversity in MSG composition ranges from two to 70 species of very similar or completely different phenotypes. Yet consistency in organization is also observable in that one or a few species usually have disproportionate importance for MSG formation and/or maintenance. We propose a two-dimensional framework for understanding this diversity and consistency, concentrating on the types of interactions possible between two individuals, usually of different species. One axis represents the similarity of benefit types traded between the individuals, while the second axis expresses asymmetry in the relative amount of benefits/costs accrued. Considering benefit types, one extreme represents the case of single-species groups wherein all individuals obtain the same supplementary, group-size-related benefits, and the other extreme comprises associations of very different, but complementary species (e.g. one partner creates access to food while the other provides vigilance). The relevance of social

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information and the matching of activities (e.g. speed of movement) are highest for relationships on the supplementary side of this axis, but so is competition; relationships between species will occur at points along this gradient where the benefits outweigh the costs. Considering benefit amounts given or received, extreme asymmetry occurs when one species is exclusively a benefit provider and the other a benefit user. Within this parameter space, some MSG systems are constrained to one kind of interaction, such as shoals of fish of similar species or leader–follower interactions in fish and other taxa. Other MSGs, such as terrestrial bird flocks, can simultaneously include a variety of supplementary and complementary interactions. We review the benefits that species obtain across the diversity of MSG types, and argue that the degree and nature of asymmetry between benefit providers and users should be measured and not just assumed. We then discuss evolutionary shifts in MSG types, focusing on drivers towards similarity in group composition, and selection on benefit providers to enhance the benefits they can receive from other species. Finally, we conclude by considering how individual and collective behaviour in MSGs may influence both the structure and processes of communities.

Key words: co-evolution, evolution of sociality, interspecific communication, keystone species, mimicry, mutualism, public information, species networks

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I. INTRODUCTION

Mixed-species animal groups (MSGs), defined as moving groups of animals that form through interspecific attraction, are observed in diverse taxa and habitats. They range from

oceanic crustacean swarms (Ohtsuka *et al.*, 1995), to fresh- and saltwater fish shoals (Lukoschek & McCormick, 2000; Pajmans, Booth, & Wong, 2019), aquatic and terrestrial groups of social mammals (porpoises, ungulates, and primates; Stensland, Angerbjörn, & Berggren, 2003) and flocks

of birds across many types of aquatic and terrestrial habitats (Harrison & Whitehouse, 2011; Colorado, 2013). MSG participation can increase the body condition and fitness of participants (Dolby & Grubb Jr., 1998; Jullien & Clobert, 2000; Srinivasan, 2019), while providing a variety of antipredator, foraging, and other benefits (Morse, 1977; Sridhar, Beauchamp, & Shanker, 2009; Goodale, Beauchamp, & Ruxton, 2017). Frameworks defining the fundamental underpinnings of animal sociality and community structure increasingly include MSGs (Graves & Gotelli, 1993; Seppänen *et al.*, 2007; Harrison & Whitehouse, 2011; Gil *et al.*, 2017, 2018; Sridhar & Guttal, 2018). Hence, the protection of MSGs is considered crucial for community approaches to biodiversity conservation (Veit & Harrison, 2017; Zou *et al.*, 2018), and wildlife or domestic animal management (Odadi *et al.*, 2011).

Scientific commentary on MSGs appeared as early as Bates (1863) and became a central focus of field studies on terrestrial birds at the turn of the 20th century (e.g. Swynnerton, 1915), and later in the century for other taxa [e.g. for primates (Gautier & Gautier-Hion, 1969)]. Taxon-specific research has hampered the emergence of an integrated framework for understanding MSG interactions. However, the groundwork is now provided by Goodale *et al.* (2017), a global review of the prevalence, distribution, and size of MSGs in different taxa and habitats (covering >580 published articles on fish, mammals and birds). The authors describe a remarkable diversity of MSGs, ranging in size from just two species to as many as 70 [the latter extreme described by Munn, 1985 for tropical birds]. Member species can sometimes be so phenotypically similar to each other as to suggest mimicry, such as plumage resemblances in avian MSGs (Moynihan, 1968; Beauchamp & Goodale, 2011), and fish MSGs (Sazima, 2002). MSG participants can also be from completely different taxa, exhibiting contrasting morphologies and behaviours, such as mongooses and birds (Rasa, 1983), tuna, dolphin, shark and seabirds feeding over fish schools (Au, 1991), and birds, mammals, reptiles, and even fish following primates (Heymann & Hsia, 2015).

Despite the extraordinary diversity in MSG composition, consistency exists in their organization across taxa in that one or a few species are typically of greater importance in the formation and/or maintenance of MSGs. Terms given to such species are diverse across disciplines, including ‘catalysts’ or ‘initiating’ species, if important to formation (Hoffman, Heinemann, & Wiens, 1981; Harrison *et al.*, 1991) and ‘leading’ species, if important to maintenance (Goodale & Beauchamp, 2010). ‘Core’, ‘central’, ‘nuclear’, and ‘important’ are among the terms given to species when they are invariably present, or their role is influential but not precisely specified, or when they affect both MSG formation and maintenance (Moynihan, 1962; Munn & Terborgh, 1979; Lukoschek & McCormick, 2000; Sridhar, Jordán, & Shanker, 2013; Marthy & Farine, 2018). Individuals of other species make decisions to join, follow, or remain in MSGs depending on the presence of these important species. Their

systemic role then must derive from benefits that other species extract from them specifically, rather than from the MSG as a whole. What kinds of benefits important species provide has not been well reviewed across taxa (but see Chapter 7 in Goodale *et al.*, 2017).

Our objective is to provide a framework that captures this diversity and consistency among MSGs, allowing us to categorize them based on the most important drivers of variation in composition and organization. In keeping with previous work, we define MSGs as moving animal groups that owe their existence to social interactions between species (Powell, 1985; Goodale *et al.*, 2017). By contrast, stationary phenomena, such as mixed-species aggregations or mixed-species colonies, are structured, in addition to interspecific interactions, by resource patches or predator-free space, respectively. Nevertheless, many of the organizing principles of MSGs (e.g. information provision), and many of the benefits traded in them, also apply to these stationary phenomena [see Chapter 2 in Goodale *et al.*, 2017 and Boulay *et al.*, 2019], and we will thus continue to mention them throughout this review. Table 1 provides a glossary of key terms used herein.

II. A GENERAL FRAMEWORK FOR CLASSIFYING RELATIONSHIPS IN MSGs

(1) Pairwise interactions in MSGs

In the framework represented in Fig. 1, each point in the xy parameter space represents the relationship between a pair of individuals in a group. The x axis represents a gradient in asymmetry of the nature of benefits obtained (or provided), while the y axis represents asymmetry in the amounts of benefits transferred between providers and users.

Along the x axis, when two individuals in an MSG provide similar kinds of benefits to each other we call the benefits ‘supplementary’ (type S, Fig. 1). That is, each associate supplies additional amounts of the same benefit, irrespective of its species identity (Table 2). We could also characterize supplementary benefits as derived from the group as a whole, and they may be related to the overall size of the group (Elgar, 1989; Beauchamp, 2014). The relationship between two individuals of different species exchanging supplementary benefits is similar to that between two conspecific individuals in a single-species group (SSG in Table 2 and Fig. 1; Sridhar & Guttal, 2018).

By contrast, benefits that are qualitatively different in their nature are ‘complementary’: an individual of one species provides a benefit that the other species cannot access on its own or without costs on its own (type C, Fig. 1). In other words, the species are different in ‘their resource-generating efficiency’ (Barker *et al.*, 2017). Associates can provide complementary benefits of different classes: for example, anti-predator benefits derived from one species, and foraging benefits from the other; or, in extreme asymmetrical systems, one associate can provide a benefit while the other provides

Table 1. Glossary of terms

Terminology	Definition
Activity matching	The process by which species adjust their behaviour in order to persist in the same MSG with other species (Sridhar & Guttal, 2018).
Benefit-providing species (or 'provider')	A species whose individuals provide a greater proportion of benefits in an MSG than the average MSG member. The opposite role is referred to as a 'benefit user', or simply 'user'.
Catalyst species	A species that tends to initiate MSGs, and hence synonymous with 'initiating species' (Hoffman <i>et al.</i> , 1981). A species that is not a catalyst can be called a 'joiner'.
Central species	A species that tends to be central (the hub of connections) to social networks in MSGs (e.g. Marthy & Farine, 2018).
Community informant	A species that provides copious and situationally-specific public information that it influences many other species, and hence the overall community (Sieving <i>et al.</i> , 2010).
Complementary benefits	Benefits traded between social partners that are different from each other. Each individual provides something that is lacking in its partner.
Core species	A species that is almost always present in a MSG system (Munn & Terborgh, 1979).
Leading species	A species that is followed in MSGs by other species.
Mixed-species aggregation	A non-moving group including individuals of multiple species that exists because of a resource, among other reasons.
Mixed-species colony	A non-moving group including individuals of multiple species that exists because of predator-free space, among other reasons.
Mixed-species group (MSG)	A moving group including individuals of multiple species that exists because of attractions between the members (Goodale <i>et al.</i> , 2017).
Nuclear species	A species that is 'important to the cohesion or initiation' of MSGs (Moynihan, 1962), and hence synonymous with 'important' species. The non-nuclear species can be called an 'associate' (Goodale & Beauchamp, 2010), 'attendant' (Moynihan, 1962), or 'satellite' (Dolby & Grubb Jr., 1998).
Oddity effect	The effect by which predators are better able to detect, attack or capture prey if the prey appear different from the average phenotype of the group.
Relevance	The use of information derived from one species by another species (e.g. for finding appropriate food or deploying appropriate predator-avoidance tactics) (Magrath <i>et al.</i> , 2015). Generally, relevance will increase for more similar species.
Sentinel species	A species that is particularly disposed to detecting predators and providing public information about them.
Supplementary benefits	Benefits traded between social partners that are similar in nature. Each individual that joins a group adds a similar, additional benefit.

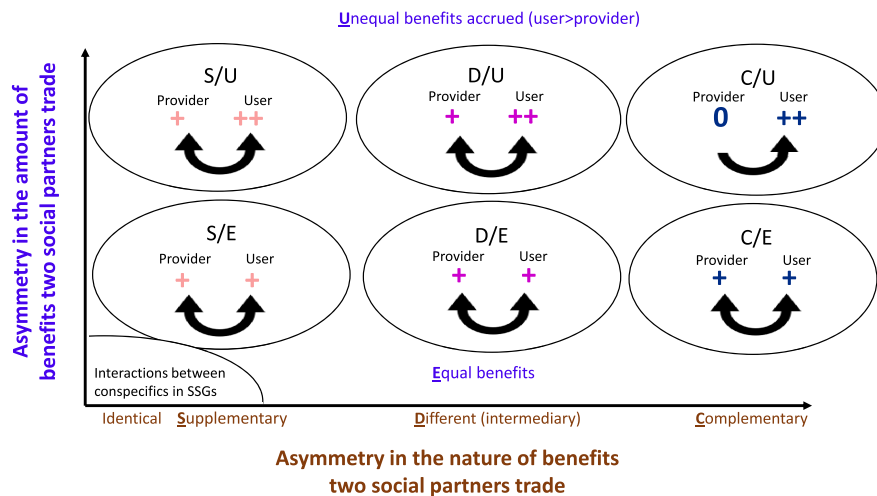


Fig. 1. A framework to classify interactions between pairs of individuals in single-species groups (SSGs) and mixed-species groups (MSGs). The x axis represents asymmetry in the nature of the benefits traded between the partners, ranging from similar, supplementary benefits (S, light red), to highly complementary ones (C, dark blue). The y axis represents the division in the total amount of the benefits transferred between the partners, ranging from providers and users benefitting equally (E), to them sharing asymmetrically (U), with the user benefiting more. The x axis is categorical, with different (D, medium purple) benefits being intermediary between S and C and providing continuity across the categorical axis; the y axis is quantitative and continuous (from 50:50 benefit division to 100:0).

Table 2. Processes by which individuals in groups exchange benefits, and patterns among such groups in their phenotypic similarity, relatedness, and traits. Groups include both single-species groups (SSGs) and mixed-species groups (MSGs), with the same categories shown in Fig. 1 [supplementary (S), different (D) and complementary (C)]. Examples of MSG types refer to Fig. 2

	Group category	SSGs Intraspecific	S Interspecific	D Interspecific	C Interspecific
Process	Benefits	Similar benefits		Within-class benefits (i.e. both anti-predation, or both foraging)	Between-class benefits (i.e. one anti-predation, the other foraging)
	Mechanism	Supplementary (group-size related)		Complementary, or one partner complementary and the other supplementary	Complementary
	Examples (anti-predation)	Dilution of risk		Complementary vigilance	Access to food traded for increased vigilance
Pattern	Examples (foraging)	Vacuum cleaner effect		Cooperative, complementary hunting	
	Phenotypic similarity	High	Fairly high	Medium	Low
	Phylogenetic relatedness	Same by definition	High	Medium	Low
	Traits underlying benefits	Similar	On average similar	Medium	Highly dissimilar
	Traits underlying costs	Similar	Can be dissimilar	Can be dissimilar	Uncertain
Empirical examples of MSG systems: birds			Mixed-species bird flocks: provider species that is intraspecifically gregarious but provides no species-specific benefits.	Mixed-species bird flocks: provider species that makes available species-specific benefits in terms of information or food accessibility	Mixed-species bird flocks: sentinel species that catches food beaten by other species
Empirical examples of MSG systems: fish			Surgeonfish or parrotfish associations		Goatfish and wrasse associations

nothing. A category of different relationships (type D, Fig. 1) lies between the categories of supplementary and complementary benefits, in which the associates may provide benefits of the same class (e.g. anti-predation), but that are qualitatively different from each other (e.g. vigilance for different predators). Although the x axis can be viewed as a categorical system, the intermediary nature of type D provides some continuity along the axis.

While we focus on interactions between individuals of different species, we acknowledge that intraspecific variation may play a key role in MSGs. The literature on MSGs has often treated species as homogenous entities, but this overlooks important aspects of intraspecific variation (Farine, Garroway, & Sheldon, 2012). Individuals of different sexes, ages, body conditions, or personality types (e.g. axes of boldness, exploration and aggressiveness) may accrue or provide different benefits or costs within any group (Aplin *et al.*, 2013; Sih *et al.*, 2015), and particularly in mixed-species groups (Suhonen, 1993; Hino, 2000). Moreover, different kinds of roles could be played by individuals that are

otherwise equivalent (e.g. a trade between two individuals of vigilance and grooming; Noë & Hammerstein, 1995). However, understanding all interactions within groups is beyond our scope (see Krause & Ruxton, 2002; Ward & Webster, 2016). Although we aim to present the most general framework applicable to interactions between any two individuals, we will focus our attention on interspecific interactions. Yet, when we discuss relationships at the species level, we note that the discussion could also be relevant to a phenotype within a species (e.g. one sex, one age group). In the future, empirical tests of the relative extent of intraspecific *versus* interspecific variation in behaviour or benefit provisioning (e.g. Farine & Milburn, 2013) are needed under different conditions to test their relative importance in structuring MSGs.

The y axis of the framework represents asymmetry in the amounts of benefits, a continuous, quantitative gradient, ranging from equal (E) relationships at the bottom to unequal (U) relationships at the top, with the latter interactions representing provider–user relationships. This concept of a

providing species is similar to Moynihan (1962)'s notion of a 'passive nuclear species' that is followed/joined by other species because other species benefit by associating with it (Contreras & Sieving, 2011). By contrast, an 'active nuclear species' that recruits other species to follow/join it would form more-mutualistic relationships [see examples of drongos that attract their associates (Goodale & Kotagama, 2006; Baigrie, Thompson, & Flower, 2014) and zebra that may attract other species with their stripes (Ireland & Ruxton, 2017)].

Provider–user interactions can vary in their relationships based on where they are located on the asymmetry of benefits (x) axis. Towards the left of Fig. 1, all individuals could provide similar supplementary benefits, but a provider species could have more individuals than other species, and so, at the species level, the provider creates a larger percentage of the benefits than other species (MSG type S/U). Alternatively, a provider species can be one that, due to its different capacities, provides a benefit that a user species cannot obtain on its own or from conspecifics (MSG types D/U and C/U; Barker *et al.*, 2017; Sridhar & Guttal, 2018; Pajmans, Booth, & Wong, 2019).

In contrast to interactions with unequal benefits, many MSGs occur in which associates are equivalent in their roles as provider or user (MSG types S/E, D/E, and C/E). Further, intermediary positions are possible on the y axis, where benefits are weakly asymmetrical – both species are providers, but one species provides more than the other. This axis must integrate benefits and costs: some relationships with dominant or aggressive species will bring particular costs (e.g. kleptoparasitism of one species by the other; Brockmann & Barnard, 1979), and these will need to be incorporated into determining how asymmetric a relationship is in MSGs. Finally, interactions in MSG could vary not only in their asymmetry, but also in the overall magnitude of the benefit transferred, that is, how much this benefit transfer influences the fitness of the interacting species. Our framework visualizes the direction of the interaction (which of the two interactors most benefits), but not the magnitude. Yet the magnitude becomes critical when thinking about the importance of any particular species to the overall MSG system, as in Section II.2.

Stochastic factors also structure relationships in MSG. We expect that MSG composition would be relatively more stable, or structured, in complementary associations, since the benefits of the association come from the specific traits of particular species. On the other hand, group composition should trend increasingly towards the stochastic in supplementary systems, where species are essentially redundant in their contributions to the group. Similarly, if one species provides most of the benefits in an MSG, the composition of the remainder of the group may be relatively unimportant to group function and could vary with the species pool, as seen in the composition of terrestrial bird MSGs in human-disturbed habitats (Maldonado-Coelho & Marini, 2004; Sridhar & Sankar, 2008; Colorado & Rodewald, 2015b; Mammides *et al.*, 2018; Zou *et al.*, 2018).

(2) Moving from pairwise interactions to MSG systems

In Fig. 2, we plot real-world MSG systems (e.g. flocks of birds or shoals of fish) in the same xy parameter space where data points represent the relationship between two species. Understanding pairwise interactions (as in Fig. 1) can lead us to understand a whole system (Fig. 2). The figure only includes those interactions thought to be important to the structure of the MSG (i.e. we plot provider–user but not user–user interactions), assuming that users matter less to the function of the MSG than providers (although they influence species richness, and can add costs such as competition). While the presence of one species can affect the relationship between two (or more) other species [e.g. the presence of gulls (*Chroicocephalus ridibundus*) and golden plovers (*Pluvialis apricaria*) (Barnard & Thompson, 1982); and greater racket-tailed drongos (*Dicrurus paradiseus*) influence the relationship between treeshrews (*Tupaia nicobarica*) and sparrowhawks (*Accipiter* sp.) (Oommen & Shanker, 2009)], the type of MSG is largely comprised of the kinds of pairwise interactions found within it. Thus, species that are providers of large-magnitude benefits in many relationships will end up playing important roles in the MSG.

Some MSGs can consist of relationships derived entirely from one section of the parameter space (see Fig. 2). For example, schools of parrotfish or surgeonfish are all of similar size or colour where interactions are supplementary and equal (MSG type S/E). The similar size of school members may allow them to move at the same speed (Krause, Godin, & Brown, 1996). Similar colouring may be adaptive because it reduces the 'oddity effect', in which predators are better able to detect, attack and capture individuals that appear different from the average phenotype in the group (Landeau & Terborgh, 1986; Jeschke & Tollrian, 2007; Pereira, Feitosa, & Ferreira, 2011). Another kind of fish group is a provider–user commensalism which is complementary and unequal (MSG type C/U). Here, the provider species, the dash dot goatfish (*Parupeneus barberinus*), disturbs the substrate, providing food for users such as checkerboard wrasses (*Halichoeres hortulanus*) that do not provide any benefits in return (Lukoschek & McCormick, 2000; Sazima *et al.*, 2007).

Other MSGs, however, may include different types of interactions, and even a single species can be involved in interactions in different regions of the parameter space (see Fig. 2). Terrestrial birds prefer to join flocks of species that are phylogenetically similar and have similar traits, especially in body size and diet, perhaps because they are vulnerable to the same predators, or because they need to travel at the same speed to obtain shared resources (Sridhar *et al.*, 2012; Colorado & Rodewald, 2015a; Péron, 2017; Mammides *et al.*, 2018). In fact, a majority of interactions in these flocks may be supplementary (Sridhar *et al.*, 2012). At the same time, most terrestrial bird MSGs have gregarious leading species (Goodale & Beauchamp, 2010). If the leader provides no species-specific benefits but is simply numerous, its

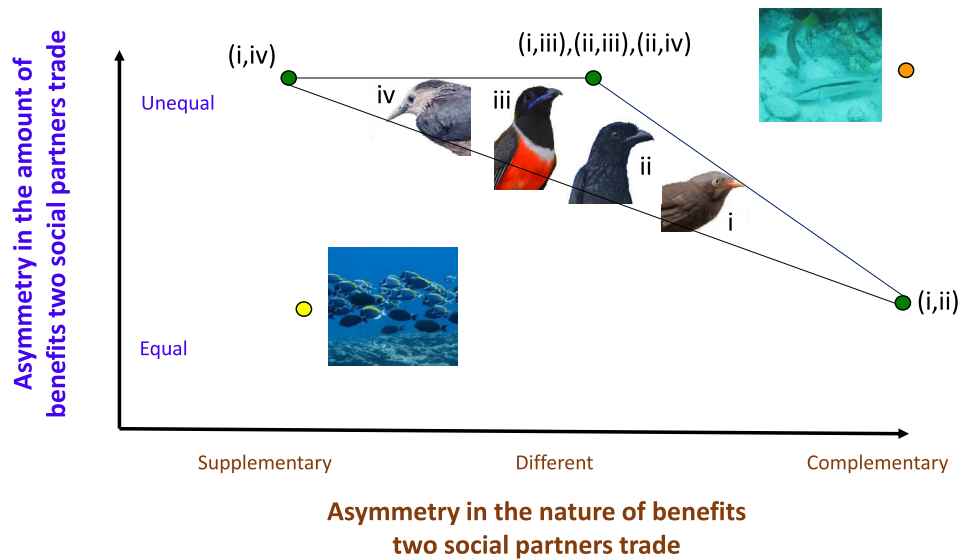


Fig. 2. Examples of mixed-species group (MSG) types, plotted in the parameter space of Fig. 1. For simplicity, each point is here an interaction between species. Different interactions within the same MSG are connected with a line and are of the same colour. In some MSG systems, all relationships are confined to a part of the parameter space, whereas in others, different kinds of relationships can be included in the same MSG. Yellow: an MSG of surgeonfish (*Acanthurus leucosternon* and *A. auranticavus*), matched in size and shape, although not colour. Orange: dash dot goatfish (*Parupeneus barberinus*, provider) and checkerboard wrasse (*Halichores hortulanus*, user), associations. Green: a mixed-species bird flock, including highly dissimilar kinds of interactions – (i) provider: orange-billed babbler (*Turdoides rufescens*, OBBA); (ii) sentinel species: greater racket-tailed drongo (*Dicrurus paradiseus*, GRTD); (iii) fly-catching user: Malabar trogon (*Harpactes fasciatus*, MATR); (iv) gleaning user: white-faced starling (*Sturnornis albofrontatus*, WFST). Photographs of surgeonfish by Rucha Karkarey, and goatfish-wrasse by Anne Theo. Photographs of OBBA (Iain Robson), GTDR (Lip Kee Yap), and MATR (Vinay Bhat) from Wikimedia Commons, and that of WFST by Eben Goodale.

relationship with a follower is supplementary, but unequal (type S/U). If that leader does give a species-specific, complementary benefit, and the following species provides only dilution, this is a combination of a complementary (the leader's contribution) and supplementary (the follower's contribution) relationship that due to its intermediary nature classifies as a type D association with unequal benefits (D/U). There can also be a complementary association with equal benefits (C/E) such as in a relationship between the leader and a 'sentinel species' that catches disturbed insects (Sridhar & Shanker, 2014b) yet provides vigilance in return (Goodale & Kotagama, 2005a; Srinivasan & Quader, 2012; see Sections III3a and V1).

Overall, MSG systems will vary in several properties. First, MSGs vary in their distribution across the nature of benefits (x) axis, and whether they include relationships based on supplementary or complementary benefits, or both. Second, MSGs vary in the collective asymmetry in the amount of benefits (y) axis, from systems that include no clear providing species (least asymmetrical), to those that have one species that is consistently a large-magnitude provider to many users (most asymmetrical). Systems that have multiple providers can be considered as multipolar, and thus at the system level, the MSG may be considered symmetrical. Finally, MSGs vary in properties such as their species richness, which can have consequences for processes within MSGs, a topic we will return to in Section VI.

(3) Different processes underlie the structure of different MSG systems

Our framework facilitates description; any relationship between individuals in MSGs should fit inside the parameter space of Fig. 1, and MSG systems will map as combinations of the interactions within them as in Fig. 2. But the framework is also useful in hypothesizing the processes shaping the types of MSGs frequently found in nature, in part, by locating these processes on the nature of benefits axis. MSGs involving phenotypically dissimilar species are more likely to lie towards the right of the x axis, correlated with phylogenetic differentiation (Table 2). The greater the difference in species' phenotypes, the greater the capacities each has to provide unique, and hence complementary benefits.

Interspecific competition also changes across the x axis, increasing with phenotypic similarity, and is likely to play a significant role in single-species groups and supplementary MSGs, but little or no role at all in complementary MSGs. In the continuum between single-species groups and supplementary MSGs, competition among individuals will increase with phenotypic similarity, with the greatest competition possible occurring in single-species groups (Fig. 2 in Seppänen *et al.*, 2007; Fig. 1 in Sridhar & Guttal, 2018). Indeed, the relaxation of competition is a benefit of MSGs as compared to single-species groups. In the latter, the benefits of similarity (e.g. similar body size, providing similar activity speed and

risk dilution), and the costs (competition) are linked: as similarity increases, there are both greater benefits and greater costs. However, in MSGs, species can match some traits that provide benefits, while remaining different in others that impose the cost of competition (Sridhar & Guttal, 2018). So, for example, an animal can forage with another species that is the same body size (and gain dilution of risk), but that uses a different foraging technique, resulting in less competition (Colorado & Rodewald, 2015a). Another potential cost of similarity in MSGs is disease or parasite sharing (González *et al.*, 2014; Holt & Bonsall, 2017); parasite sharing likely operates in a way similar to competition, with greater phylogenetic similarity increasing costs, because species with shared evolutionary histories host similar parasite communities and infectious agents are spread more easily among phylogenetically similar organisms (Poulin, 2010).

The advantages of similarity for participants in MSGs derive from supplementary benefits and individuals can accrue many of the same benefits as could be provided in single-species groups. If information transfer is the basis between two species interacting, the more similar to each other they are, then the more they will share the same predators or resources, and the more 'relevant' is the information provided by one species to the other (Seppänen *et al.*, 2007; Magrath *et al.*, 2015). Also, the species are better matched in how they forage and move, and hence incur lower costs in 'activity matching', that is, changing behaviours to remain associated with other species in MSGs (Hutto, 1988; Darrah & Smith, 2013; Sridhar & Guttal, 2018). MSGs may actually be preferable to single-species groups (or the only choice) in cases where intraspecific sociality is limited (e.g. animals are intraspecifically territorial and cannot form SSGs, or they provide reproductive competition to each other, as reviewed by Sridhar & Guttal, 2018). Meanwhile, decreasing relevance and activity matching may explain why taxonomically diverse taxa do not often group together and derive similar benefits from each other. For example, birds and mammals may not usually group together for anti-predator benefits as these species often travel at different speeds and are vulnerable to different predators.

MSGs based on complementary benefits would appear to have very different mechanisms of assembly (or selective regimes) from those based on supplementary benefits. Here the associations would seem to be 'by-product' mutualisms, where the species-specific behaviour of one species is then used by another species at a low or non-existent cost (Sachs *et al.*, 2004). It is unlikely that interspecific competition derived from phenotypic similarity plays any role in the evolution of these MSGs. This kind of group is particularly associated with foraging; foraging efficiency is limited in MSGs of similar species because competition will increase with group size. Foraging-associated relationships underlie most reports of complementary, unequal (type C/U) relationships (commensalism) in MSGs (see Section III4a). The kinds of relationships in complementary, equal (type C/E) MSGs may be quite similar to symbioses in which one partner provides nutrition (e.g. pollination, seed dispersal, or ants interacting with aphids or caterpillars; Douglas, 2015).

III. BENEFITS PROVIDED IN MSGs

Various reviews of benefits obtained in MSGs are available [reviews that span multiple taxa or habitats include Morse, 1977, Diamond, 1981, Terborgh, 1990, Harrison & Whitehouse, 2011 and Goodale *et al.*, 2017]. Our treatment differs in that we separate supplementary and complementary components. We focus on anti-predator and foraging-related benefits, which are the most common benefits in MSGs (Morse, 1977). These two classes of benefits are not mutually exclusive and in fact are functionally inseparable, as animals suffering increased perceived risk of predation are forced to concentrate more on vigilance, reducing their foraging efficiency (Sullivan, 1984; Gil *et al.*, 2017). More occasionally, MSGs are known to provide other benefits such as thermoregulation, avoiding desiccation, reducing energetic costs, or lowering intraspecific social aggression (Goodale *et al.*, 2017).

(1) Supplementary benefits related to reducing predation risk

Perhaps the most common supplementary anti-predator benefit is risk dilution, i.e. reduction in predation risk arising simply from an increasing number of individuals in a group. Each individual in the MSG here provides an identical benefit, if all individuals/species are equally vulnerable to predators. This identical benefit requires similarity; if some individuals have a different phenotype, they may be more vulnerable due to the oddity effect [see Beauchamp, 2014 and Section V2]. A related supplementary anti-predation benefit is the 'selfish-herd' effect, wherein participants on the periphery of the group try to move towards the centre (Hamilton, 1971). Any other anti-predator benefit postulated as occurring in single-species groups as a consequence of increased group size – greater vigilance created by more eyes and transmitted through the group by alarm calls, confusion created by many individuals' responses, defence when a larger group is less vulnerable to a predator – can also apply as a supplementary benefit to MSGs (Beauchamp, 2014; Goodale *et al.*, 2017). Yet because species may differ in their capacities to be vigilant or to be aggressive, we will also return to these ideas in Section III3.

(2) Supplementary benefits related to increasing foraging efficiency

Hypotheses about supplementary foraging benefits include the idea that a large group of foragers could overcome the territorial defences of solitary individuals ('gang theory', Diamond, 1981), and participants in a group may have knowledge of where the group has gone and temporarily depressed food levels ('foraging efficiency theory', Diamond, 1981; which we will refer to as the 'vacuum cleaner effect' 1981). Another class of foraging benefits in MSGs involves social copying (one individual observing and copying another of a different species) of foraging locations or techniques

(Krebs, 1973). Similarity is important here: in order to benefit from social copying, the copier must share the same prey and the method of capturing prey as its heterospecific model. All individuals in a MSG can also produce food through disturbance of the substrate, as in producer–scrounger models (Giraldeau & Beauchamp, 1999). However, because such disturbance can be very particular to certain species, we discuss it mostly as a complementary benefit.

(3) Complementary benefits related to anti-predator benefits

(a) Sentinel species

Species that have high vigilance and transmit information about predators are referred to as sentinel species (Munn, 1984; Terborgh, 1990; Pagani-Núñez *et al.*, 2018). Usually they produce alarm calls in response to moving and threatening predators, which generate freeze, flee or hide behaviours in species privy to their meaning (Lima & Dill, 1990; Jones & Sieving, 2019). While often vocal, alarm information available to eavesdroppers can also be visual, chemical, or multimodal, as in the case of birds taking flight (Lima, 1994), chemical signalling in fish (Chivers & Smith, 1998), or the way in which a giraffe's posture can act as a cue about predators (Schmitt, Stears, & Shrader, 2016).

Sentinel species' capacity to transmit information about predators may be derived from different traits. Social species that have many individuals per MSG may be more prone to make alarm calls, as they collectively provide many eyes per MSG, and may also be more likely to make costly signals for their conspecific audience due to kin selection or investment in pair-bonded mates (Goodale *et al.*, 2010; Goodale & Beauchamp, 2010). Further, species that live in socially dynamic and persistent single-species groups (e.g. the parid family of birds; Szymkowiak, 2013) may exhibit greater vocal and cognitive complexity (Sewall, 2015). In turn, this supports higher vocal entropy, or capacity to encode a range of situationally specific information, concerning (for example) the class or species of predator, or its behaviour and imminence of attack (e.g. Seyfarth, Cheney, & Marler, 1980; Griesser, 2008; Ouattara, Lemasson, & Zuberbühler, 2009; Sieving, Hetrick, & Avery, 2010; Freeberg & Lucas, 2012; Suzuki, 2014). Other species that might be especially 'good' (sensitive, timely, accurate, truthful or a combination of these) at alarm calling include those that: (i) have to be vigilant to find prey (e.g. fly-catching birds; Munn, 1984) or can remain vigilant as they forage (Fernández-Juricic, 2012); (ii) inhabit a good vantage point (e.g. tall ungulates; Fitzgibbon, 1990; Schmitt *et al.*, 2016); (iii) use different strata of the forest (either high or low) and thus detect a particular suite of predators (Bshary & Noë, 1997; McGraw & Bshary, 2002; Astaras *et al.*, 2011); and (iv) have excellent sensory acuity and hence better ability to gather information relevant to predation (Fernández-Juricic, Erichsen, & Kacelnik, 2004). Alarm-calling sentinel species are especially attractive to species that share the same predators, or to which they are

related (potentially making the signals easier to learn or be recognized), as has been recently shown in the African ungulate literature (Schmitt *et al.*, 2014; Meise, Franks, & Bro-Jorgensen, 2018).

(b) Mob-attracting species

Animals' responses to mobbing calls are usually the opposite of alarms, attracting others towards predators that are stationary or detected in a state in which they are not of immediate danger (Marler, 1955; Curio, 1978). Mobbers can be overtly aggressive, involving close approaches and physical attacks, and therefore mobbing can be effective in making a predator leave the area (Pavey & Smyth, 1998; Crofoot, 2012), or falter when attempting predation [see Pitman *et al.*, 2017 and Adams & Kitchen, 2018 for two examples of multiple species producing this effect]. Although species that do not participate in MSGs also mob, MSG members, and especially sentinel species, are often initiators or central species for mobbing gatherings, due to high vocal production and complexity (Turcotte & Desrochers, 2002; Krams, Krama, & Igaune, 2006; Langham, Contreras, & Sieving, 2006; Sieving *et al.*, 2010). Although what makes species exhibit high propensity to generate and/or attend mobs requires more study, gregarious species would seem to be pre-adapted because of their motivation to protect or impress conspecific members of the group.

(c) Enforcers

Enforcers are species that can offer physical protection against predators. They are represented in bird and mammal MSG systems by species such as drongos (Dicruridae) and capuchins (Cebinae), respectively, due to these species' overall high level of aggression toward predators, including physical contact (Melville, 1991; Frechette, Sieving, & Boinski, 2014). Most published descriptions of aggression by these species have to do with conspecific interactions (e.g. Gardner *et al.*, 2015); they deserve more attention in the MSG context. Enforcer functions are also presented in the context of stationary nesting associations of prey birds near formidable predator species or even stinging insects (Bogliani, Sergio, & Tavecchia, 1999; Quinn & Ueta, 2008).

(d) Species that are differentially preferred, detected or attacked by predators

A final kind of complementary predation 'benefit' a species can provide is when its presence offers a disproportional dilution of risk to other species. In antelope (Fitzgibbon, 1990) and fish (Mathis & Chivers, 2003) followers benefit by joining species that are preferred by predators, as they are attacked less. Contreras & Sieving (2011) suggest that the attractiveness of the tufted titmouse (*Baeolophus bicolor*) as a passive leader in terrestrial bird MSGs of North

America may derive, in part, from its high vocal production and ubiquitous presence in flocks; the presence of these conspicuous birds may dramatically dilute attack risk to other species. One could also hypothesize that the opposite situation could occur, in which a species preferred by predators or detected easily joins a group of heterospecifics. As long as such a species remains in the minority, a predator might not attack such a group, or might have difficulty finding the preferred prey among many non-preferred ones (Goodale, Ruxton, & Beauchamp, 2019).

(4) Complementary benefits related to foraging

(a) *Beating (disturbing food)*

Making food more accessible by disturbing the substrate or vegetation (hereafter 'beating') is a major class of complementary benefits in MSGs. This kind of benefit drives most associations between highly dissimilar species, including commensal and mutualistic relationships. As examples, we present the following phenomena roughly organized by how dissimilar the species are: (i) seabirds following animals (tuna, dolphin, diving seabirds) that drive fish into a ball and close to the surface (e.g. Au & Pitman, 1986; Clua & Grosvalet, 2001); (ii) birds, and occasionally other animals, following army ants (e.g. Willis & Oniki, 1978; Willson, 2004); (iii) birds following ungulates (e.g. Fernandez *et al.*, 2014); (iv) diverse animals following primates (Heymann & Hsia, 2015), or, more occasionally, treeshrews (Oommen & Shanker, 2009); (v) marine animals following goatfish (Lukoschek & McCormick, 2000; Sazima *et al.*, 2007); (vi) wading birds following large and active wader species (e.g. Courser & Dinsmore, 1975); and (vii) freshwater waterbirds following large species like swans (e.g. Källander, 2005). As the followers are dissimilar to the leaders in these examples, they do not offer much dilution (e.g. they may attract different predators), and the associations can be viewed as commensalisms. Followers may even be parasitic on the leaders, as has been demonstrated in the case of army ant followers (Wrege *et al.*, 2005).

A few other relationships based on beating feature more symmetrical benefits, such as alarm-calling fly-catching birds following gleaning species in terrestrial bird MSGs (Munn, 1986; Sridhar & Shanker, 2014b; also see Section V1), and associations between mongooses and birds (Rasa, 1983; Ridley, Child, & Bell, 2007), where foraging benefits are exchanged for vigilance. In addition, as mentioned above, dissimilar animals such as eels and groupers (Bshary *et al.*, 2006), or coyotes and badgers (Minta, Minta, & Lott, 1992), can hunt together, making use of their complementary hunting methods (MSG type D/E). In these cases, one species (the badger or the eel) tends to move prey out of, or away from, the substrate, while the other makes the prey seek shelter in the substrate. In this case, neither species could be called more of a provider or user than the other, as they effectively drive the prey towards each other.

(b) *Recruitment to resources*

Are some species particularly good at finding food? This attractive idea was originally advocated as a way of explaining colonies of birds (Ward & Zahavi, 1973), yet little evidence has appeared to date in the form of heterospecific information transfer of this type (Richner & Heeb, 1995). The hypothesis tends to apply to clumped, abundant resources, and hence better to aggregations, whether stationary or moving. Examples include: (i) seabird species that find fish driven together by tuna or diving birds; these initiating or catalyst species are often the first at the scene and provide a public cue to the presence of fish by flying ('circling') above the area (e.g. Hoffman *et al.*, 1981); (ii) obligate antbirds that are used by less-dependent species to find food (Martínez *et al.*, 2018b); (iii) snowy egrets (*Egretta thula*) that are thought to be especially good at finding pools with fish, explaining why they are attractive to other wading species (Caldwell, 1981; Smith, 1995); and (iv) carcass-scavenging birds, in which some species search earlier in the day or more efficiently, or advertise their finds by circling (Buckley, 1996; Kane *et al.*, 2014; Orr, Nelson, & Watson, 2019). Recent work on terrestrial bird MSGs using artificial feeders has suggested that those species with especially loud calls (Suzuki, 2012), or those that cache seeds (Farine *et al.*, 2015) may be used by others to find food. Another potential example of foraging recruitment driving MSG organization is squirrel monkeys (*Saimiri sciureus*) that have large home ranges following capuchin monkeys (*Cebus apella*) that have small home ranges, apparently to exploit the knowledge of the latter on the local distribution of resources (Podolsky, 1990).

(5) Species that can provide multiple complementary benefits

As pointed out by Gil *et al.* (2017), most animals do not exclusively produce information about foraging, or about predation, but they can serve as an information source about both. For example, tufted titmice and other birds in the Paridae family make many vocalizations associated with alarm, as discussed above, but also vocalize when food is encountered (Suzuki & Kutsukake, 2017), and are almost continuously noisy making a variety of contact calls that encode variation in perception of risk (Sieving *et al.*, 2010; Pagani-Núñez *et al.*, 2018). Such species that provide a large amount of situationally specific information can be considered 'community informants' (Schmidt, Dall, & van Gils, 2010; Hetrick & Sieving, 2012; Jones & Sieving, 2019). Such constantly vocal species could also use silence as a form of information: an abrupt stop in their information might show that some unusual risk is at play, yet not call attention to themselves as an alarm call would. Continuous calling thus forms a kind of 'all clear' signal or 'watchman's song' (see Dapper, Baugh, & Ryan, 2011 for amphibians, Kern & Radford, 2013 for mammals, and Baigrie *et al.*, 2014 for birds).

An interesting contrast can be made between MSG systems that have one leading species that provides multiple benefits, like tufted titmouse-led systems, and systems where these benefits are provided by separate species. In South Asia, foraging benefits (e.g. social copying, beating) and alarm calls may be associated with some gregarious leading species, but sentinel species additionally provide vigilance (Goodale & Kotagama, 2005a). So perhaps one could think of some leading species being ‘specialist benefit providers’, whereas others might be ‘multiple benefit providers’.

(6) Supplementary benefits made available by a particular species

We identify a few instances where benefits are supplementary and yet they still are associated with certain species more than others. We present two such cases: (i) when a gregarious species provides more supplementary benefits than other species because of the number of its individuals per MSG; and (ii) when a species is conspicuous and thus a good indication of MSGs, so that other species join or follow it to find an MSG. In fact, these two instances may be interconnected, as gregarious species might be especially conspicuous (Goodale & Beauchamp, 2010).

In the sections above, we argued that species that have multiple individuals per MSG may be particularly apt to provide information about predation or foraging because of the requirements of their conspecific audience (type D/U or type C/U). However, a species could be a benefit provider by being numerous even if its individuals did not behave differently from those of other species. Squirrel monkeys are an example of such a supplementary and unequal (type S/U) benefit provider, with up to five times the number of individuals as the capuchins they associate with (Podolsky, 1990). Terrestrial bird MSGs are often led by gregarious species (Goodale & Beauchamp, 2010). In certain situations, animals may follow gregarious species if they do not have enough individuals to make their own single-species groups. This phenomenon also has been reported across taxa, in animals ranging from mysids (Wittmann, 1977), to dolphins (Frantzis & Herzing, 2002) and primates (Fleury & Gautier-Hion, 1997). In primates, single-species groups have limits to their size due to intraspecific social forces, and by offering the possibility of larger groups, MSGs can offer more supplementary benefits than can single-species groups (Heymann & Buchanan-Smith, 2000). Something similar may be happening in fish, where species that are intraspecifically gregarious to different degrees such as surgeonfish, parrotfish, and wrasses, may come together to form larger MSGs (K.Shankar and A.Theo, personal observations).

Regarding conspicuous species, in the recruitment to resources section, we mentioned a few examples (circling seabirds or scavengers, loud birds at feeders) of species especially capable of recruiting heterospecifics to resources. But the idea that conspicuous species could be an indicator of an MSG itself is a broader concept, in that the benefits that

the joining/following species could gain need not be exclusive to foraging benefits or even anti-predator benefits. We see these kinds of benefits as a mix of supplementary (group-derived) and complementary (conspicuousness is species-specific) components. Sometimes the conspicuous species’ behaviour is aimed at conspecifics, and eavesdropped on by other species, but at other times these species’ signals may have evolved to recruit heterospecifics, as in the case of the ‘active nuclear species’ discussed in Section III.1.

IV. INVESTIGATING SPECIES ROLES IN MSGs AND THE BENEFITS IMPORTANT SPECIES PROVIDE

In essence, our framework differentiates supplementary benefits that individuals in MSGs can gain from the MSG itself, from complementary benefits that may be gained from specific species (or a specific phenotype within a species). Further, we see such complementary benefits as the underlying reasons that make particular species important to MSGs. However, as argued in Section III.6, the situation is not quite so simple: important species could be giving supplementary benefits, but just more of them at the species level when they are gregarious, or such species simply could be indicators of MSGs. In this section, we review the ways in which we can (i) measure species roles – their importance to MSGs – and (ii) also understand what benefits are being transferred. A further question about important species in MSGs is, (iii) how dependent are other participants on them? It is particularly necessary to address this question if important species are to be targeted in conservation plans in order to protect the whole MSG community (Zou *et al.*, 2018). Finally, (iv) another aspect of species’ roles to investigate is at the level of MSG systems and their properties: why might some systems or particular habitat types have multiple important species, whereas others have just one, or none at all?

(1) Temporal and spatial observational data

In seabird MSGs that assemble around fish resources, catalyst species are identified by looking at which species first find the patch (Hoffman *et al.*, 1981; Camphuysen & Webb, 1999). For terrestrial bird MSGs, a variety of methods can define which species lead them. For example, one can measure the percentage of movements of the group, or pairs of species, that are led by an individual of a particular species (Morse, 1970; Contreras & Sieving, 2011). Another approach is to look for species that are represented consistently towards the front of the group (e.g. Kotagama & Goodale, 2004). Movement and horizontal organization data can be particular clear-cut when observing only two-species MSGs (Sridhar & Shanker, 2014a). These approaches may not be able to detect the importance of sentinel species that move behind beating species; however, temporal data might reveal that users join sentinel species.

Non-random spatial associations between species inside a MSG, i.e. nearest neighbour analyses, can also indicate strong relationships (Sridhar & Shanker, 2014b; Gu *et al.*, 2017). If individuals are marked, leadership can also be studied at the individual level, and as radio-tracking methods improve, data will be obtained on relative positions and movements of individuals in real time (see Chapter 9 in Goodale *et al.*, 2017).

Temporal/spatial data are particularly useful in determining what benefits joiners/followers are seeking in MSGs. One can count how many times A comes before or follows B, and how many times the reverse situation occurs. When associated with species traits, such analyses can suggest which particular benefits an initiator/leader could provide (e.g. Sridhar & Shanker, 2014b). When combined with data on the behavioural change of joiners/followers in the presence or absence of leaders, results can be even more convincing. For example, in terrestrial bird MSGs one could study the vigilance of a following species with or without a leading species to demonstrate that anti-predator benefits are transferred (e.g. Sullivan, 1984). Or one can look at the feeding rates of following species when proximate to leaders (e.g. Hino, 1998).

(2) Statistical analysis of co-occurrence in observational data

A very different approach to measuring the importance of particular species to MSGs is to investigate statistical associations between species, i.e. co-occurrences in MSGs. For example, observed MSGs can be compared to null models based on the abundances of all animals in an area, to see which nuclear species have the most positive, non-random associations with other species (Srinivasan, Raza, & Quader, 2010). Species (or even particular individuals) can be identified that are highly connected and hence central in social network analyses (Farine *et al.*, 2012; Sridhar *et al.*, 2013; Mammides *et al.*, 2018; Marthy & Farine, 2018; Meise, Franks, & Bro-Jorgensen, 2019). One disadvantage of these methods is that the directionality of the relationships may not be clear: for example, species with high centrality (Sridhar *et al.*, 2013) may actually be close associates (primarily followers) of leading species (Sridhar & Shanker, 2014b). Multi-site studies are especially important to investigate whether important species retain their role in different places and across different habitat and land-use gradients (Gram, 1998; Mammides *et al.*, 2018). Indeed, we might expect that important species would remain more constant in their centrality over time and space if their benefits go beyond supplementary ones, and if they provide large-magnitude benefits that user species can use under many different conditions. Similar to spatial data, statistical approaches can be combined with species traits to suggest what benefits are provided (e.g. Srinivasan *et al.*, 2010; Sridhar *et al.*, 2013). Statistical, multi-site approaches may also be able to identify whether other species are able to persist when putative important

species are absent, measuring the dependency of the relationship.

(3) Experimental approaches

Decisions to join an MSG are experimentally tractable by simulating the presence of a species. For visually oriented species, such as seabirds or waders, models have been used to test which species initiate aggregations (e.g. Caldwell, 1981; Bairos-Novak, Crook, & Davoren, 2015). For acoustically oriented species, playback can be used to simulate the presence of putative nuclear species of MSGs to see how many and which species are attracted (e.g. Mönkkönen, Forsman, & Helle, 1996; Goodale & Kotagama, 2005b; Langham *et al.*, 2006; Cordeiro *et al.*, 2014), or to understand whether species are listening to each other (Windfelder, 2001). Again, combined with species traits, attraction towards simulated cues can be used as evidence of what benefits species are seeking in MSGs (e.g. Goodale & Kotagama, 2005b; Gu *et al.*, 2017; Martínez *et al.*, 2018b). However, there are limitations to the applications of the methods; for example with playback, species that are not very vocal or loud cannot be simulated, or those that make a lot of alarm calls could attract species that mob predators, but do not usually participate in MSGs (Krams & Krama, 2002).

Another experimental method involves the actual removal of a species, and this has the advantage of being able to show cause-and-effect relationships. Removal experiments can demonstrate behavioural changes in the remaining group members that suggest what benefits important species provide (Cimprich & Grubb Jr., 1994; Dolby & Grubb Jr., 1998; Krams, 2001; Martínez *et al.*, 2018a). For example, after removal of an important species, increases in individual vigilance and decreased risk taking (Dolby & Grubb Jr., 2000), or changes in the thickness of the vegetation individuals choose to forage in (Martínez *et al.*, 2018a), can suggest that the important species was an anti-predator benefits provider. By looking at changes in body condition (Dolby & Grubb Jr., 1998) or, even better, survival, fitness, or population growth (Ramirez, 1984), these sorts of experiments can also measure the dependency of one species on another. Yet field experiments have limitations too: removals not only alter the presence or absence of a species but also the number of individuals in the group, and that can be problematic if the leader is gregarious, as many are. The experiments are also difficult to implement, as they require conditions where other individuals do not immediately fill the vacancies in MSGs.

(4) Future directions

We believe creative new designs using established experimental methodologies can help test hypotheses about species importance to MSGs (Table 3). For example, removal experiments could have one treatment in which all the individuals of the putative important species are removed, and in contrast to that, another treatment in which a few individuals

Table 3. Potential new directions in mixed-species group (MSG) studies linked to (a) identifying species roles and benefit providers and (b) further understanding MSG evolution and their relationship to issues of community ecology

Subject	Potential new direction
(a) Species roles and benefit providers	<p>Playback experiments that test reaction to the MSG as a whole, as well as to individual species.</p> <p>Reciprocal removal experiments that compare MSGs reduced by one or more species to one in which the same number of individuals has been reduced, but some individuals of all frequent species remain.</p> <p>Observe how species roles or system properties (e.g. the number of important species) change if experimentally increase food resources or introduce predators or simulations of predators.</p> <p>Observe how species roles or system properties change across environmental, biological, or human-disturbance gradients.</p> <p>Observational, multi-site studies of species roles and associations in taxa other than forest bird MSGs and in different habitats, including anthropogenically disturbed ones.</p>
(b) Evolution and community ecology	<p>Quantifying the effect of MSGs on species range limits along elevational gradients.</p> <p>Use MSGs to explore the effects of social information on species co-existence and for realized niche space.</p> <p>Quantitative cross-taxa studies that look at the prevalence of MSGs (compared to single-species groups and other forms of sociality), understanding the contribution of both environmental and species trait variables.</p> <p>Studies of whether some functional groups in MSGs (e.g. sallying, alarm-calling species) are increased in areas where MSGs are dominant.</p> <p>Studies of whether MSG participation affects colonization or extinction on islands or fragments.</p> <p>More tests of phylogenetic clustering/overdispersion paradigm on MSG systems.</p> <p>Studies of what happens to prey items when MSGs are absent or lost (e.g. trophic cascades).</p>

of most participating species in the MSG are removed, retaining some individuals of all species, so that the resulting group size is the same as in the first treatment. This kind of experiment could determine whether the important species is truly providing a complementary benefit. Playback experiments can adjust the numbers of individuals of a species that is simulated (Martínez *et al.*, 2018b), and thereby study similar issues. Another useful playback design would be to include one treatment of the vocalizations of the MSG as a whole, in addition to treatments featuring putative important species. This would help distinguish whether attraction to an important species was merely because that species is a good indication of a MSG.

Other types of experimental procedures may prove helpful to identify species roles and which, or how many, species in an MSG are providers. For example, resource supplementation (e.g. Berner & Grubb Jr., 1985; Székely, Szép, & Juhász, 1989; Kubota & Nakamura, 2000) and the experimental addition or simulation of predators (e.g. Székely *et al.*, 1989; Noë & Bshary, 1997; Martínez *et al.*, 2017) have been used to investigate the benefits of MSGs. New studies should address what happens to species networks when environmental conditions are changed in such ways (Mokross *et al.*, 2014; Borah, Quader, & Srinivasan, 2018). If the role of a species is diminished when food is more available or when predator risk is lower, then it is likely a provider of complementary benefits (provided that MSG size is standardized). The addition of novel feeding patches (Farine *et al.*, 2015) or foraging tasks (Freeberg *et al.*, 2017) can also determine the role of particular species in information transmission.

Additionally, comparative-causal studies can take advantage of environmental (e.g. altitude or habitat variation),

biological (e.g. species richness), or human disturbance gradients over which species roles (or even propensity to join MSGs) change (Gentry *et al.*, 2019). A variety of questions can be investigated using such gradients, including understanding what happens when an important species drops out at some point on the gradient (Goodale *et al.*, 2015), or, at the system level, documenting how system properties (e.g. how many important species are present, or how asymmetrical a system is) change across the gradient.

A final recommendation for future work is to increase the diversity of taxa and habitats studied. Current studies of important species in MSGs are predominantly focused on terrestrial birds, and more studies on other kinds of birds (grassland or waterbirds), or on non-avian animals, would help increase the generalizability of results. Further, work in anthropogenically disturbed areas might change how we understand what factors (e.g. altered predation environments) influence the asymmetry of species relationships in MSGs (Colorado & Rodewald, 2015b).

V. THE EVOLUTION OF MSGs: IS THERE MOVEMENT BETWEEN MSG TYPES?

Once there is a categorization system for the kinds of relationships seen in MSGs, one can ask whether relationships might be expected to move between categories over evolutionary time. In Fig. 3, and below, we illustrate two potential drivers of such movements: (1) responses by providers of complementary benefits in MSGs to claim a more equitable division of benefits from

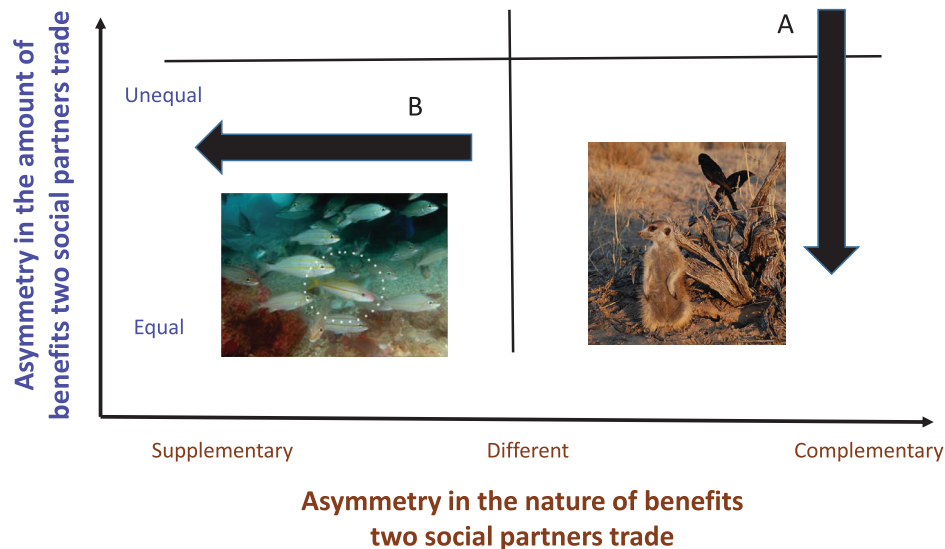


Fig. 3. Drivers that may underlie changes between mixed-species group (MSG) types over evolutionary time. A: providers may evolve so that their share of benefits are more equitable with their associates in MSGs, if such changes are possible. An example of a complex co-evolved system is shown between meerkats (*Suricata suricatta*), and fork-tailed drongos (*Dicrurus adsimilis*) (Flower *et al.*, 2014; photograph by Tom Flower). B, species that regularly interact in MSGs may become more similar to other members, so that the ‘oddy effect’ is less severe and so that their activities (e.g. movement speed) are better matched. An example of potential mimicry in fish is shown in which yellow goatfish (*Mulloidichthys martinicus*, in dotted circle) joins a group of tomtate grunt (*Maemulon aurolineatum*) (Pereira *et al.*, 2011; photograph by the authors, published under a Creative Commons license).

their associates, and hence more symmetric interactions, and (2) selection for convergence of species in MSGs.

(1) Evolution towards more symmetrical trading of benefits

Providers in MSGs may be trapped in their roles if there is no real cost to them and/or the benefits they make available to other species are an incidental ‘by-product’ of their species-specific behaviour (Sachs *et al.*, 2004) for which the individual or intraspecific benefits outweigh any consideration of the use of the behaviour by other species. In other instances, there may be costs to providers from users, such as kleptoparasitism, but removing the heterospecifics (e.g. by aggressively attacking them or escaping from them; Johnstone & Bshary, 2002) may be even more costly or impossible. In the case where users are costly, we might expect the most asymmetrical relationships to persist when providers are relatively smaller and subordinate to users, or less mobile than them, and hence cannot resist the associates’ presence and behaviour.

In other cases, however, there may be room for evolutionary movement, and we envision greater movement towards increased symmetry rather than in the opposite direction primarily because there are more systems that are asymmetrical than are fully mutualistic (e.g. in the examples of complementary benefit provisioning, Sections III3–5). Increased symmetry may come either from increasing benefits through co-evolved behaviour (Sachs *et al.*, 2004; Barker *et al.*, 2017), or

exactng more costs on associates by manipulating or even deceiving them (Mokkonen & Lindstedt, 2016; Lucas *et al.*, 2018).

A good example of a symmetrical relationship that seems a balance of both mutualism and manipulation is given by sentinel species in terrestrial bird MSGs that catch insects disturbed by heterospecifics, specifically antshrikes (*Thamnomanes* spp.) in the Neotropics, and drongos in the Palearctic (drongos also associate with a variety of mammal species; e.g. Ridley *et al.*, 2007; Oommen & Shanker, 2009). While evidence is mixed as to whether these species lead MSGs – sometimes they may follow beating species – other species certainly listen to their alarm calls (Munn & Terborgh, 1979; Ridley & Raihani, 2007; Oommen & Shanker, 2009; Radford *et al.*, 2011; Martínez *et al.*, 2016), and such anti-predation information has high fitness value. At the same time, the sentinels manipulate other species by making false alarm calls (Munn, 1986; Satischandra *et al.*, 2010) and, for drongos, these false alarms include the imitations of other species’ alarm calls (Flower, 2011). Drongos have also been reported to use the imitation of non-alarm calls to initiate MSGs (Goodale & Kotagama, 2006). There is evidence of an interspecific arms race between drongos and their associates here: as other species habituate over time to the imitated false alarms, drongos may rotate through imitations of many species to keep their imitated alarms effective (Flower, Gribble, & Ridley, 2014). Yet overall, the basic swap of access to food for

vigilance provides the foundation for mutualism (Srinivasan & Quader, 2012), and there is evidence that the sentinels can increase their value to their partners by conducting sentinel behaviour (Radford *et al.*, 2011; Bairrie *et al.*, 2014), and even alarm-calling about predators that are mostly dangerous to their associates and not to themselves (Ridley *et al.*, 2007).

Co-evolution leading to persistent mutualism has been also demonstrated in cleaner fish, although they do not fit our definition of a moving MSG since cleaning stations may be stationary, and the cleaners are aggregating around a resource. One model species, the bluestreak cleaner wrasse (*Labroides dimidiatus*), prefers to eat fish mucous rather than parasites, which constitutes cheating (Grutter & Bshary, 2003). In order to control cheating, the client fish can ‘punish’ the cheater by stopping the interaction or even chasing the cleaner (Bshary & Grutter, 2005). It can also assess how cooperative cleaning fish are by watching them clean other clients, and then choose partners that are cooperative (Pinto *et al.*, 2011). Further, cleaners behave more cooperatively in the presence of watching clients, showing that the ability of clients to switch partners ensures the mutualism of the interaction (Pinto *et al.*, 2011).

In both these examples (fly-catching species and cleaning fish) the ability to interact repeatedly with the same individuals of the partner species could stabilize the interaction by reducing the propensity to cheat or to extract the maximum from the partner without offering anything in return (Axelrod & Hamilton, 1981). Sachs *et al.* (2004) describe two ways in which cooperation may be maintained even when it imposes costs: ‘partner fidelity’ occurs if the producer invests in a partner that then benefits it in return, and ‘partner choice’ occurs if the producer chooses a partner that is especially cooperative. As described above, cleaning fish have been shown to use partner choice (Pinto *et al.*, 2011). A hypothetical example of partner fidelity would be if drongos that make honest alarm calls are allowed closer to their associates, and therefore benefit more from access to food. Evidence for the importance of repeated interactions in cleaning fish is that a species that has a large home range, bicolor cleaner wrasse (*Labroides bicolor*), is more cooperative in areas where it is more likely to encounter clients again in the future (Oates, Manica, & Bshary, 2010). Familiarity between individuals of different species has also been shown to increase reciprocal altruism in mobbing among terrestrial birds (Krams & Krama, 2002) and is thought to be a pervasive characteristic of most MSGs (e.g. Johnson, Masco, & Pruett-Jones, 2018).

(2) Evolution towards greater similarity in MSGs

A second potential evolutionary force affecting MSGs is a movement towards convergence. Again, we see the preponderance of movement towards similarity rather than away from it partially because there are more systems that can move in this direction – striking resemblances among species in MSGs are rarely seen, although they attract attention. Also,

as pointed out in Section II3, in MSGs similarities can develop in some characteristics (e.g. visual patterning), while niche differentiation is maintained in other traits (e.g. foraging ecology).

One mechanism that may be particularly important in promoting similarity, especially in visual resemblances, has been alluded to earlier: predators appear confused by many similar individuals, and in larger groups their capture rates decline (Neill & Cullen, 1974; Ruxton, Jackson, & Tosh, 2007). This ‘confusion effect’ has been found to be fairly widespread in predators that hunt visually (Jeschke & Tollrian, 2007), and can be enhanced when all the prey individuals react to an attack by moving together (Ioannou, Guttal, & Couzin, 2012); it is related to the oddity effect discussed earlier because phenotypic differences among group members reduce confusion (Tosh, Jackson, & Ruxton, 2006). Several other forces may also act to impose similarity in MSGs: species that are similar may share the same predators, may be able to communicate better amongst each other (Moynihan, 1968), and be well-matched in their activities, such as their swimming speed (Krause *et al.*, 1996). By contrast, competition and shared enemies (i.e. parasites; Holt & Bonsall, 2017) may work against similarity, but these forces might be less of an issue when the risk of predation is paramount.

Evidence of a drive towards similarity is demonstrated by resemblances between species in MSGs that have sometimes been considered mimicry. Plumage similarities within terrestrial bird MSGs have been noticed for half a century (Moynihan, 1968), and the majority of putative mimics do indeed resemble their models in flocks more than species that are phylogenetically related, or live in the same habitats, at least to human eyes (Beauchamp & Goodale, 2011). ‘Protective mimicry’ among species all preyed upon by the same predators has also been reported in MSGs of fish (Pereira *et al.*, 2011). Another sort of mimicry in fish is when predator species resemble harmless species and hence are allowed to get closer by prey species; such ‘aggressive mimicry’ may work best when the mimicking predators group with their models (Sazima, 2002). Less-specific kinds of resemblances among species, such as in body size in fish (Krause *et al.*, 1996) or birds (Sridhar *et al.*, 2012) just could be a result of assortment in ecological time, rather than mimicry. The forces of similarity may also be most important when there is a gregarious provider species that presents a model for other species to copy; for example, one might expect such forces in Asian terrestrial bird MSGs, which typically have at least one gregarious species, and not in Amazonia, where only a few individuals per species participate in MSGs (Powell, 1985; Goodale *et al.*, 2015).

(3) Future directions

Many aspects of the two evolutionary shifts discussed above require greater inspection: for example, it would be useful to compare MSG groups in the symmetry of interactions between sentinels and their various kinds of associates; resemblances among MSGs should be investigated in their geographic variation, tying hotspots of similarities to drivers

(e.g. predation) or potential models. But thinking more generally, MSGs may be excellent systems to look at the underlying evolution of sociality. By definition, associating with heterospecifics must arise from individuals accruing direct fitness benefits [for the evolution of cooperation through direct fitness, see also Lang & Farine, 2017 on cooperative hunting]. In turn, this reduces the possible drivers of sociality, compared to other situations that must also consider indirect fitness through kinship [but see Barker *et al.*, 2017, for some ways in which genetic correlations between species can influence the evolution of cooperation, or how even inclusive fitness could be involved, if heterospecific benefits affect kin]. MSGs are models for understanding what species traits lead to the evolution of cooperation, such as how the vigilance of sentinel species has led to their complicated relationships with their associates. Indeed, by incorporating functional traits with ancestral state reconstruction (Brumfield *et al.*, 2007; Martínez *et al.*, 2016), we can explore the degree to which different traits, including sociality, are under stabilizing selection. Specifically, we can ask how conserved sociality is in MSGs, and what traits influence whether species participate in or are important to MSGs, or particular types of MSGs. MSGs are also models to understand environmental influences on sociality; a good example is the investigation of Grubb Jr. (1987) describing how weather influences the choices of grouping intra- or interspecifically. Ultimately, one could use a model selection approach to test whether phylogeny, species-specific traits or environmental conditions best predict MSG participation, and to identify covariance patterns across variables to predict sociality.

VI. DO MSGs INFLUENCE OVERALL COMMUNITY STRUCTURE AND FUNCTION?

(1) Species diversity in MSGs: causes and consequences

Where will MSGs be particularly dominant and species rich? For each kind of MSG, different abiotic and biotic variables will be important. For example, for terrestrial bird MSGs, there is evidence that higher predation pressure (Thiollay, 1999) and lower food availability (Grubb Jr., 1987; Mangini & Areta, 2018) increase participation. The richness of the relevant participant pool imposes an upper limit on the diversity of MSG systems (Colorado & Rodewald, 2015b): the richness of terrestrial bird MSGs will be higher than those of porpoise MSGs, in part, because there are more potential species to associate; within taxonomic groups, the richness of tropical bird MSGs may be greater than temperate bird MSGs, following the global patterns of biodiversity.

However, we also believe that the diversity of MSGs is related to the functional framework laid out in Section II. When influenced by co-evolution, partners have requirements that are more specific and only a few species with the required traits can be involved. Hence, we see low diversity in complementary, mutualistic MSGs. Also, the strong

similarity required for species to associate in supplementary MSGs will limit the diversity of those groups. The highest diversity will thus be found in MSGs where more than one kind of interaction can occur (e.g. birds), or in MSGs with redundant species that give supplementary benefits, but not too similar to compete with each other (MSG type S/E; again birds, as they have high foraging specialization compared to other groups such as primates; Terborgh, 1990). High diversity can also occur when a provider makes available benefits to a wide variety of species (complementary or different, but unequal benefits – MSG types D/U and C/U). For example, for MSGs that depend on the provider making prey available to other species through their disturbance, the scale of the disturbance, and the variety of the kinds of prey made available, is clearly a large factor regulating the species diversity of users.

Does species diversity have impacts on MSG functioning? From the point of view of complementary benefits, each new species in an MSG system may bring its own specific capacities. For example, different species may have different abilities to detect and alarm call about predators (Goodale & Kotagama, 2005a), or problem-solving abilities when encountering a novel foraging task (Freeberg *et al.*, 2017). Thus, more diverse MSGs may have higher cumulative abilities to avoid predators or find food. In the future, it would be useful to investigate further whether diversity of the system as a whole is matched by the diversity of important species. A larger number of important species that have some redundancies among each other could lead to greater resilience of the system in the face of disturbance (Oliver *et al.*, 2015).

(2) The importance of MSGs for community processes

Species interactions involved in MSGs may have consequences for community ecology at several different spatial scales. At the largest scale, one can ask whether species in MSGs influence their members' distributional ranges. Many studies have attempted to address whether species interactions (particularly competition) influence species range limits (e.g. Connor & Simberloff, 1979; Case & Taper, 2000); however, whether (positive) social interactions shape species range distributions is a relatively unexplored question. In most MSGs, the exchange or receipt of benefits classifies as ecological facilitation, where species interact to the benefit of at least one participant without harm to any. As such, strong conceptual and experimental evidence exists in support of ecological facilitation among species, including range expansion when a benefit user is in the presence of a provider in relatively harsh environments (Bulleri *et al.*, 2016). Evaluating the degree to which species in MSGs coincide in range distributions, compared to non-participating species in the same areas, would be a valuable avenue of future research (Goodale *et al.*, 2015).

MSGs have been suggested by Harrison & Whitehouse (2011) to be a potential example of 'niche construction', in which the activity of some species creates a new niche that

can be occupied by other species. In other words, MSGs could allow the expansion of the fundamental niche of a species to a larger realized niche (Odling-Smee, Laland, & Feldman, 2003). The phenomena reviewed here in which some species provide foraging opportunities to others clearly fit under this category. But Harrison & Whitehouse (2011) make a subtler point that the social relationships that species make in MSGs alter the selective landscape for participating species. For example, one created niche in terrestrial bird MSGs may be that of sallying species that benefit by catching disturbed insects and also provide vigilance to other species. One could then hypothesize that in areas where MSGs are dominant, there might be more of these kinds of fly-catching, alarm-calling species, or more species that forage in occluded microhabitats (e.g. probing in dead leaves) and rely on their vigilance. Another potential community-level effect may occur when terrestrial bird MSGs hold interspecific territories (e.g. in many Neotropical flocks), keeping some participating species' densities lower than they might otherwise be, and hence acting as a force for increasing community diversity (Powell, 1989), and allowing species to co-exist (Graves & Gotelli, 1993).

One can also examine the degree of phylogenetic clustering at the community level within MSGs and their surrounding communities. The paradigm of using phylogenetic clustering as evidence of environmental filtering, and phylogenetic overdispersion as evidence of interspecific competition, has become widely used in community ecology (Webb *et al.*, 2002). Some evidence suggests phylogenetic clustering in MSGs, perhaps indicating a weakening of competition in these generally mutualistic systems (Gómez *et al.*, 2010; Sridhar *et al.*, 2012; Péron, 2017). However, overdispersion could still occur in MSGs if complementary benefits strongly influenced their structure (Péron, 2017), and these kinds of studies should now be attempted in a variety of MSG systems, acknowledging that phylogeny is a coarse way of looking at ecological similarity and the approach has some potential pitfalls (Gerhold *et al.*, 2015).

At the scale of the meta-community, we see MSGs as important influencers of what habitats their participants might be able to move through and live in. Travelling in MSGs could change the risk of moving through an unfavourable matrix, and make individuals/species better able to move between and colonize patches, and hence may be an important variable to factor into meta-community dynamics (Holyoak, Leibold, & Holt, 2005). The possibility of extinction, too, may shift under the various benefits that species accrue in MSGs. Hence, we think that the propensity for species to participate in MSGs might be an important characteristic to integrate into updated models of island biogeography and metapopulation dynamics (MacArthur & Wilson, 1967; Santos, Field, & Ricklefs, 2016). Important species in MSGs such as community informants might be especially critical in modulating this effect, with non-trophic cascades in which the important species' habitat preferences influence the habitat selection of other species (Mammides *et al.*, 2015). These cascading effects may be related to the 'landscape of fear' (Laundré, Hernández, & Ripple, 2010), in which the

presence of some important species change the perception of risk by participating species. For example, animals might be more willing to travel or forage in otherwise risky areas when an important species is present (Sieving, Contreras, & Maute, 2004; Ridley, Wiley, & Thompson, 2014), and removing such a species may change the movement and habitat use of the whole MSG, leading to an altered realized niche of the MSG (Powell, 1989; Martínez *et al.*, 2018a).

There are also potential benefits and costs of MSGs to sympatric non-participant species. If some species' habitat selection is changed through their association with MSGs as argued above, then competing species may also be affected. Even species that cannot overcome the substantial costs of joining moving MSGs may gain significant benefits from the existence of such mutualistic associations within their communities. For example, *via* eavesdropping, non-participants living in forests with bird MSGs can continuously update their local spatiotemporal maps of relevant risks (predators) and rewards (insect-rich foraging patches). Evidence supporting this idea is suggested by the large number of non-flocking animals that readily join mobbing aggregations initiated by terrestrial bird MSGs (Hurd, 1996; Langham *et al.*, 2006; Suzuki, 2016), or respond appropriately to the alarm calls produced by MSGs (Schmidt *et al.*, 2008; Magrath *et al.*, 2015; Martínez *et al.*, 2016). Some species close to, but not participating in an MSG, may also take advantage of the vigilance of the MSG to engage in activity that might otherwise be more risky (such as loudly vocalizing; H. H. Jones and F. Montaña-Centellas, personal observations). Given these potential effects of MSG systems on non-participating species, important species in MSGs can be critical facilitators for heterospecifics outside of MSGs. For example, when parid species that are described as nuclear to winter forest avian MSGs were experimentally augmented, migrant birds settled in higher densities (Mönkkönen & Forsman, 2002).

Given the evidence for community-wide impacts of MSGs, we can also conceive of ecological cascades tied to MSGs that might become apparent as they degrade. For example, the dominance of MSGs among insectivorous birds, and the enhanced foraging efficiency in MSGs, could have indirect positive effects on sympatric species *via* greater plant productivity generated by herbivorous insect population regulation (e.g. Marquis & Whelan, 1994; Vidal & Murphy, 2018). Likewise, one could imagine potential cascades generated by the absence of ungulate MSGs on African plains, or altered fish dynamics if seabird MSGs were disrupted. Thus, besides serving as bellwethers of changing land use and climate (Mammides *et al.*, 2015; Veit & Harrison, 2017; Zou *et al.*, 2018), emergent properties of MSGs may buffer animal communities undergoing change or trigger further cascades.

VII. CONCLUSIONS

- (1) A vast literature has accrued over a century on a wide variety of MSGs. We define an integrative framework

for MSG organization, distinguishing between two types of benefits: group-derived supplementary benefits, in which individuals of each species make similar benefits available, and complementary benefits, derived from species-specific traits (or traits that characterize some particular group of phenotypes within a species), and usually from specific species that play important roles in MSGs. Relationships built on supplementary benefits have different selective forces acting on them than do relationships built on complementary benefits (e.g. the important role of competition for supplementary-based MSGs, but not for complementary-based MSGs).

- (2) We argue that this distinction between supplementary and complementary benefits is crucial for new insights about important species in MSGs. We must test whether important species are providing supplementary benefits (e.g. individuals of gregarious species collectively supplying a high amount of supplementary benefits, or the species acting as an indicator of an MSG), or whether their role depends on the complementary benefits they provide.
- (3) Over time, we see evolutionary forces producing convergence among participating species better to accrue supplementary benefits. Within complementary relationships, we envision co-evolutionary processes driving benefit-providers to attempt to wrest benefits from the users that associate with them.
- (4) MSGs can influence the entire community of which they are a part via various mechanisms. MSGs may influence species' distributions, with participating species having aligned distributions across environmental gradients. MSGs may create niches and influence the species diversity of communities, and/or alter the phylogenetic structure of communities. MSGs (or their important species) may shape meta-populations (and hence meta-communities) by influencing how habitat patches are colonized and whether those populations go extinct. MSGs may also influence the lives of non-participants, and produce trophic cascades if they are lost from communities.
- (5) Although many of these potential influences of MSGs on the entire community require future research, cumulatively they make the case for including MSGs as an essential component in the ecological theories that explain community-level processes for the vertebrate groups in which MSGs are common. Further, we currently know enough to include consideration of MSGs as systems into conservation and management plans.

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E. G., K. E. S., and H. H. J. co-organized the Ecosummit symposium, which also included D. R. F., I. K., A. E. M., J. M., and A. T., and coordinated subsequent discussions. The ideas developed thereby were made into a manuscript by E. G. and K. E. S., and then merged with a framework conceived of by K. S., H. S., P. B. and A. T. to form a first draft. To obtain a greater diversity of ideas, we subsequently asked for the inputs of G. J. C. Z., E. W. H., F. M.-C. and U. S. All authors then worked together on subsequent drafts.

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