



Synthesizing perspectives on the evolution of cooperation within and between species

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Cooperation is widespread both within and between species, but are intraspecific and interspecific cooperation fundamentally similar or qualitatively different phenomena? This review evaluates this question, necessary for a general understanding of the evolution of cooperation. First, we outline three advantages of cooperation relative to noncooperation (acquisition of otherwise inaccessible goods and services, more efficient acquisition of resources, and buffering against variability), and predict when individuals should cooperate with a conspecific versus a heterospecific partner to obtain these advantages. Second, we highlight five axes along which heterospecific and conspecific partners may differ: relatedness and fitness feedbacks, competition and resource use, resource-generation abilities, relative evolutionary rates, and asymmetric strategy sets and outside options. Along all of these axes, certain asymmetries between partners are more common in, but not exclusive to, cooperation between species, especially complementary resource use and production. We conclude that cooperation within and between species share many fundamental qualities, and that differences between the two systems are explained by the various asymmetries between partners. Consideration of the parallels between intra- and interspecific cooperation facilitates application of well-studied topics in one system to the other, such as direct benefits within species and kin-selected cooperation between species, generating promising directions for future research.

KEY WORDS: Competition, cooperation, interspecific interactions, mutualism, social evolution.

Cooperation occurs between conspecifics that often interact in social groups (Alexander 1974; Queller and Strassmann 2009; Bourke 2011), and between heterospecifics that interact in mutualisms (Bronstein 2015). Here, we use the term *cooperation* to refer to any interaction in which an actor confers a fitness benefit to another individual and receives an (inclusive) fitness benefit in return, since this is the key characteristic common to the many definitions in the literature (West et al. 2007). Despite this shared characteristic, the evolution of cooperation has

historically been studied separately in intra-specific and inter-specific systems with relatively minimal cross-talk between researchers in each field. Thus, the majority of work focuses either only on cooperation within species (e.g., Alexander 1974; Sherman et al. 1995; Lehmann and Keller 2006; Bergmüller et al. 2007; Rodrigues and Kokko 2016) or only on cooperation between species (e.g., Herre et al. 1999; Bshary and Bronstein 2004; Foster and Wenseleers 2006; Leigh 2010; Bronstein 2015).

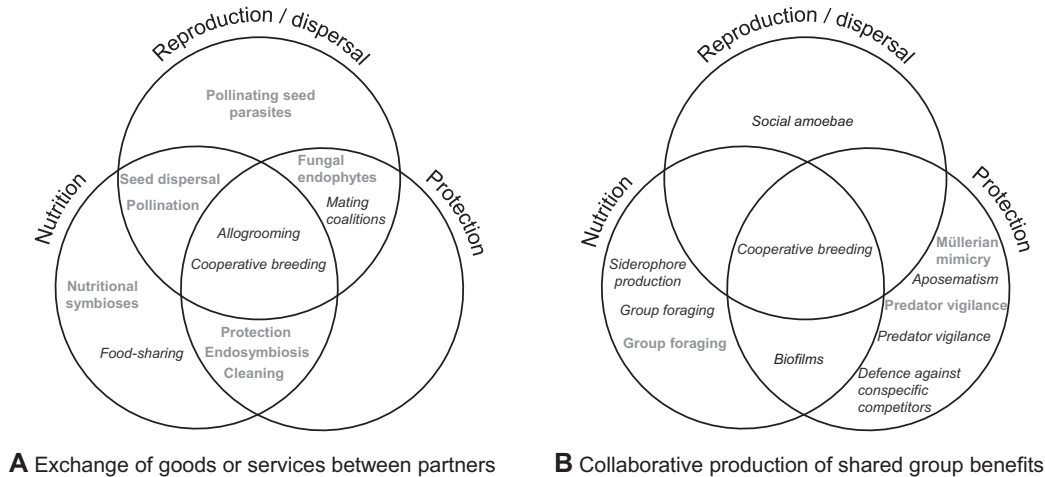


Figure 1. In both intraspecific cooperation (black *italics*) and interspecific cooperation (gray **bold text**), partners provide goods or services in terms of reproduction/dispersal, nutrition, and protection. These goods or services in turn provide direct and indirect fitness benefits. The figure highlights well-studied systems in each of these categories. Provision of benefits may take the form of (A) exchange of goods or services between partners, or (B) collaborative production of benefits shared by group members. Exchange is more common between species, while group production is more common within species. Group production of goods or services more commonly involves benefits in a single currency, while exchange often involves trading of more than one currency.

Nonetheless, a growing body of literature does address both types of cooperation (e.g., Sachs et al. 2004; West et al. 2007; Strassmann and Queller 2010; Bourke 2011; Ghoul et al. 2013). One view is that intraspecific and interspecific cooperation are a lot alike. Even the potential for genetic relatedness to favor cooperation between conspecific partners has been suggested to have an analog between heterospecifics, as extensions of inclusive fitness theory suggest that genetic correlations between species can promote interspecific cooperation (e.g., Frank 1994; Foster and Wenseleers 2006; Queller 2011). Here, we build on work bringing together perspectives on within and between species cooperation to examine whether these forms of cooperation are indeed fundamentally similar phenomena that can be interpreted using a single explanatory framework, or whether, despite superficial similarities, they are categorically different.

This review investigates the parallels between cooperation within species and cooperation between species to reveal new directions for further synthesis. Given the different research foci in each area, we explore how well-studied topics in one system can be fruitfully applied to the other (summarized in Box 1). We show that both types of cooperation confer similar benefits to partners, such as access to novel resources (Fig. 1), and are affected by common factors, particularly the extent to which partners compete for or produce the same resources (Fig. 2). We then demonstrate that both conspecific and heterospecific partners can differ from each other along several independent axes that are not necessarily linked to interspecific differences (Fig. 2). This leads to two conclusions. First, relatedness is but one of several factors determining how similar intra- and interspecific cooperation are.

Second, there is a continuum of differences between intraspecific and interspecific cooperative systems, as well as within each type of system. In sum, this review provides evidence that cooperation within species and cooperation between species are not fundamentally different phenomena, and proposes steps for identifying truly general explanations for the evolution of cooperation.

Why Cooperate with a Conspecific or Heterospecific Partner?

To transmit alleles to the next generation, individuals must acquire nutrition, protect themselves from enemies, and reproduce (and often disperse). These fitness components could be obtained by an individual on its own, but in many cases are achieved through cooperation with others. The cooperative provisioning of nutrition, protection, and reproduction takes two broad forms (Fig. 1). One is the exchange of goods or services between individual partners. The goods or services may be in the same or different currencies (e.g., reciprocal sharing of blood in vampire bats, or trading food for agonistic support in primates; see “Resource-generating efficiency” below) and partners may gain direct or indirect fitness benefits. The second form of cooperation is collaborative production of benefits shared among group members, for example, when social insect workers generate indirect fitness benefits by rearing siblings. What are the advantages of cooperating to obtain nutrition, protection, and reproduction?

First, cooperation allows individuals to acquire *qualitatively* different goods or services than they could obtain on their own. If individuals differ at a given time in their ability to produce

distinct resources, either through constitutive differences or ontological shifts, they can exchange these resources (Schwartz and Hoeksema 1998). Furthermore, even if individuals have the same resource production capabilities at a given time, combined individual efforts can lead to the generation of public goods or other shared group resources that are qualitatively different from those a single individual could produce, such as hunting big game (Hawkes 1993). Second, cooperation can also facilitate *quantitatively* greater and more efficient production of goods or services. A given amount of resource that could be obtained individually may be acquired with less time and/or energy via cooperation, due to specialization in complementary tasks and economies of scale (Queller 1997; Strassmann and Queller 2010). Third, cooperation provides two mechanisms for insurance against variability. One mechanism is via buffering or reducing variability; that is, by decreasing the probability that individuals fall below a crucial minimum threshold of resources in an unpredictable environment (Koenig and Walters 2015). For example, reciprocal food sharing may arise when individuals fluctuate between having an excess and a shortfall of food, as in vampire bats (Carter and Wilkinson 2013). Another mechanism is when cooperation facilitates additional avenues for reaping fitness benefits without reducing variability. For example, if there is a low probability of obtaining a breeding position, helping-at-the-nest can allow individuals to gain indirect fitness benefits until they can breed themselves, as in many cooperatively breeding birds (Hatchwell and Komdeur 2000).

Whether an individual cooperates to acquire nutrition, protection, or reproduction depends on the outside options for acquiring these fitness components solitarily (see “Asymmetric strategy sets, payoffs, and outside options” below), as well as on mechanisms that limit free riding such as interdependence between partners (relatedness and feedback structure). Whether cooperation confers a fitness advantage has been extensively explored elsewhere, both within and between species (e.g., Bergmüller et al. 2007; Strassmann and Queller 2010; Bourke 2011; Jones et al. 2015). Here, we ask instead, given that an individual obtains these fitness components cooperatively, will it do so with a conspecific or a heterospecific partner?

The answer to this question depends at least in part on the type of nutrition, protection, or reproduction gained from the interaction (Fig. 1). Some fitness components cannot be provided by heterospecifics, such as indirect fitness benefits from raising relatives’ offspring. These interactions often involve goods or services in the same currency for all individuals (Fig. 2), making the production of shared group benefits likely. In contrast, some fitness components cannot be provided by conspecifics, if no members of that species are able to produce or acquire certain goods or services themselves; for example, synthesis of certain nutrients or transport of gametes. In these cases, goods or services

are exchanged in different currencies. Thus, interactions between species are more commonly exchanged rather than group production and sharing. However, this difference is not discrete; some interactions between species involve sharing of group benefits (e.g., defense against predators; Fig. 1), and many conspecific partners exchange goods or services (e.g., grooming for access to food or mating opportunities; Fig. 1). These interactions are less well studied, and offer potential for further exploration of the parallels between intra- and interspecific cooperation (Box 1).

Goods or services that can be provided by either type of partner include those that depend simply on the number of individuals and not necessarily on their identity (e.g., vigilance in mixed-species foraging); that involve food or nutrients that could be produced or acquired by both species (e.g., in bacterial biofilms; Mitri et al. 2011); and that are associated with heterospecific third parties, such as defense against predators or removal of parasites (Fig. 1). When goods or services could hypothetically be provided by either a conspecific or heterospecific individual, the details of the interaction influence whether intra- or interspecific cooperation is more likely to evolve. For example, cooperation between species may evolve more readily than cooperation within a species if heterospecific partners are not also competing for the same resources (see “Competition between partners” below). However, in other cases investment in cooperation may bring additional gains to conspecific partners, such as increased status or access to mating opportunities, which may favor intraspecific over interspecific cooperation.

Factors Affecting Cooperation with a Conspecific Versus Heterospecific Partner

Many factors in addition to the provision of goods or services influence the evolution of cooperation within versus between species. Our aim is not to provide an exhaustive review, but to focus on factors that affect the evolutionary dynamics of cooperation both within and between species, and that may do so in different ways (Fig. 2). Thus, we do not discuss, for example, cheating and punishment, which pose similar issues for cooperation within and between species that have been extensively reviewed elsewhere (Ghoul et al. 2013; Jones et al. 2015; Riehl and Frederickson 2016). Instead, we explore five factors associated with asymmetries between conspecific or heterospecific partners, in each case showing how the factor promotes or impedes the evolution of cooperation within and between species.

RELATEDNESS AND FITNESS FEEDBACKS

For cooperation to evolve, there must be a mechanism that ensures that the benefits of cooperation accrue more readily to carriers of alleles encoding cooperative phenotypes than to carriers of

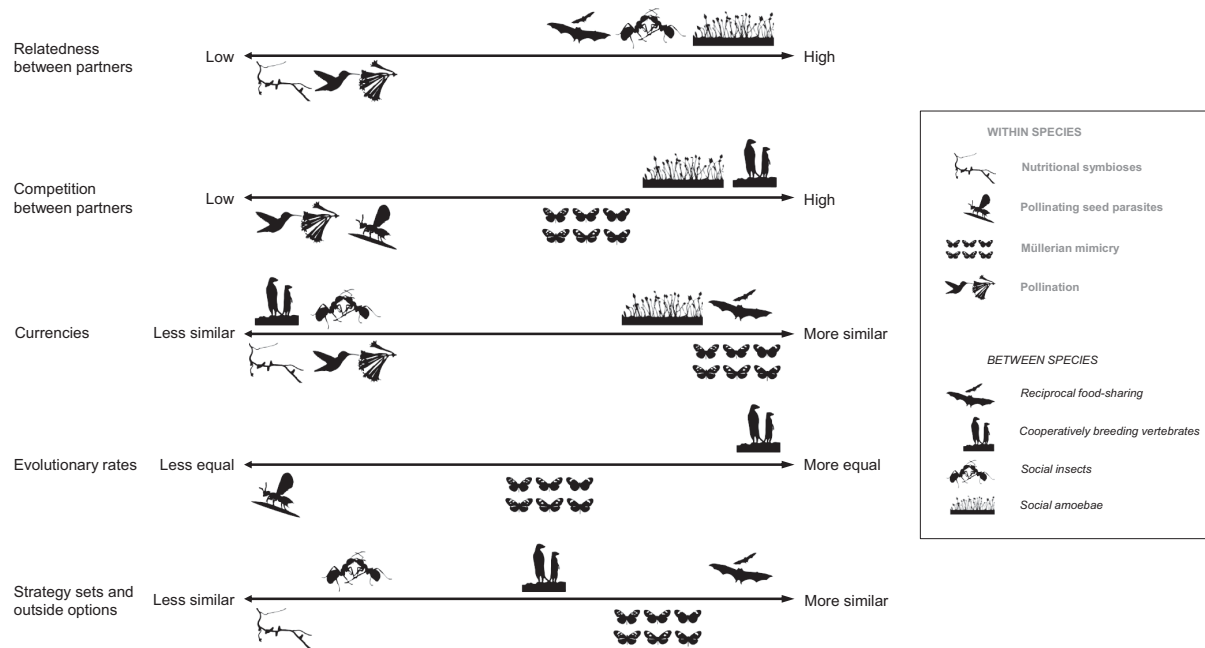


Figure 2. Cooperation within species (icons above axes) tends to have different characteristics compared to cooperation between species (icons below axes), but the differences between intra- and interspecific cooperation are continuous, not discrete. Along five largely independent axes important for the evolutionary dynamics of cooperation (relatedness between partners, competition between partners, currencies in which partners provide goods or services, evolutionary rates, and strategy sets and outside options), intraspecific systems sometimes share more characteristics with interspecific systems than with other intraspecific systems, and vice versa. Icons represent classes of well-studied examples along each axis. For simplicity, not every icon appears on every axis or along its full range on a given axis (e.g., we recognize that some social insects have low relatedness, but in general relatedness between partners is high).

alternate alleles (Fletcher and Doebeli 2009). Possibly the most obvious difference between intraspecific and interspecific cooperation is that only conspecific partners may often share a sufficiently recent common ancestor to carry alleles that are identical *by descent* (Fig. 2). As a result, an allele encoding intraspecific (but not interspecific) cooperation will sometimes also be present in the beneficiary of that cooperation, depending on population structure and any kin recognition mechanisms. Beginning with Hamilton (1964), an enormous literature has explored how genetic relatedness between partners can promote the evolution of cooperation within a species.

In contrast, the mutualism literature has emphasized direct fitness feedbacks between heterospecific partners (Sachs et al. 2004); that is, changes in the fitness of one individual that affect the fitness of its partner. In this situation, partners that are not genetically related may have a shared “stake” in one another, providing a means by which partners value each other’s fitness analogous to, but independent of, kinship (Roberts 2005). Such “partner fidelity feedback” is likely to occur when partners’ fitnesses are highly interdependent and there are minimal opportunities for choosing alternative partners (Sachs et al. 2004). When these partners have such a shared fate, one partner can increase its own (direct) fitness by promoting the fitness of its partner. While

common in cooperation between species, direct fitness feedbacks can also be important within a species, for example, for meerkat helpers feeding pups (Clutton-Brock et al. 2001). Both within a species and between species, these fitness feedbacks between partners may work in tandem with other mechanisms, such as the ability to choose or preferentially reward more cooperative partners (e.g., kin recognition, green beards, sanctions, partner choice; Roberts 2005).

Frank (1994) showed how genetic correlations between species can act in ways akin to genetic relatedness within a species to promote the evolution of cooperation. Much as relatedness (r) is a regression coefficient measuring the genetic correlation between the agents and the recipients of cooperation within a species, Frank (1994) defined a regression coefficient measuring the genetic correlation between the agents and recipients of interspecific cooperation. He then modified Hamilton’s rule for kin selection to include this between-species “relatedness,” finding that positive correlations between species favor the evolution of cooperation. However, Foster and Wenseleers (2006) concluded that the build-up of genetic correlations between species is likely to be less important than direct (i.e., phenotypic) fitness feedbacks for the evolution of cooperation between species. Queller (2011) expanded Hamilton’s inclusive fitness approach to show

how cooperation can evolve through both genetic or phenotypic correlations between partners of the same or different species. Empirically, numerous studies have estimated relatedness coefficients in intraspecific interactions, but few have measured genetic correlations between species, likely because of the technical challenges involved in doing so. Moving forward, an improved understanding of the genetic basis of cooperative traits and the spatial population structure for *both* partners in interspecific interactions (Box 1) would help resolve this issue, as would more data on phenotypic correlations between species and their fitness consequences (Queller 2011; Jones et al. 2015).

Relatedness can sometimes play an important role in cooperation between species (Box 1). When reciprocal benefits between heterospecific partners are delayed in time and space, a loss of direct feedbacks can be recovered via feedbacks delivered by a heterospecific partner to the kin of the original actor (reviewed

by Zink 2015). Thus, when cooperative partners are of different species but the benefits are indirectly returned to relatives, kin selection can stabilize cooperation between species (Frank 1994; Queller 2011). Similarly, there is growing recognition that direct fitness feedbacks are also at work in social groups; for example, reciprocity in vampire bats is a better predictor of blood donations than genetic relatedness (Carter and Wilkinson 2013). The relative importance of direct versus indirect fitness benefits in cooperation both within and between species is ripe for further investigation (Box 1), and intraspecific systems in which direct fitness benefits are especially important may be most fruitfully compared to interspecific cooperation. Thus, although the emphasis has been on relatedness in cooperation within a species and on direct fitness feedbacks in cooperation between species, it is clear that both affect the evolution of cooperation both within and between species.

BOX 1

Here, we highlight promising future directions leveraging recent research to explore the parallels between the evolution of cooperation within and between species.

Empirical studies of cooperative interactions in nature

1. *Exploring the full diversity of cooperative interactions:* Compared to resource exchange between species, collaborative production of shared resources between species (e.g., Müllerian mimicry) has been relatively neglected. Similarly, cooperative breeding (Bergmüller et al. 2007) and eusociality (Sherman et al. 1995) have received the most attention in interactions within species, even although many opportunities for cooperation within species exist outside of the context of alloparental care (Hatchwell 2010).
2. *Assessing the relative importance of direct and indirect fitness benefits in intraspecific cooperation:* There is a growing awareness that direct benefits are important in cooperation within species (Clutton-Brock 2002; Taborsky et al. 2016), but their relative importance compared to indirect fitness benefits remains an open question.
3. *The role of relatedness and population structure in cooperation between species:* Empirical studies of social microbes have shown the influence of limited dispersal on cooperation within a species (e.g., Kümmerli et al. 2009a), but few have evaluated the spatial scale of population viscosity for both partners in a mutualism, or how often the benefits of cooperation between species feed back not to the original participants, but to their kin (Frank 1994; Queller 2011; Zink 2015).

Development of new theory

1. *Relative evolutionary rates:* The conditions under which selection favors different evolutionary rates are little known, for example, what types of payoff matrices are characteristic of games in which slower evolution is advantageous? Asymmetric evolutionary rates among traits of conspecific partners also remain a largely unexplored topic.
2. *Resource-generation efficiency in interspecific cooperation:* “Transactional” models from reproductive skew theory (Reeve and Shen 2006; Buston and Zink 2009), which show how breeding can be exchanged for cooperation within social groups, could be harnessed to analyze asymmetries in resource-generation efficiency between heterospecific partners, and ultimately how the benefits of cooperation between species are divided.

3. *Value of currencies in interspecific resource exchange*: “Reproductive value” from inclusive fitness theory can be used to analyze how different classes of individuals in a population will contribute to the gene pool (Gardner et al. 2011). This is the same issue as assigning values to different goods or services traded in cooperative exchanges, particularly between species, which currently lacks a theoretical framework.
4. *Screening cooperative partners*: “Screening” has been proposed as a mechanism for choosing cooperative heterospecific partners, with the choosy partner imposing a cost on the other to enter in to an interaction (Archetti et al. 2011), but what maintains cooperation once screening costs have been paid? Could screening also function as a mechanism for social groups to choose new members?
5. *Individual variation*: Consistent behavioral differences among conspecifics have consequences for cooperative interactions (Bergmüller et al. 2010), but the effects of individual differences on cooperation between species are ripe for investigation.

Microevolution of cooperation

1. *Measuring selection on traits involved in cooperative interactions*: Linking individual traits underlying cooperative interactions to their fitness effects is crucial for understanding how cooperation evolves. We would like to see more work measuring the strength and type of selection on and heritabilities of cooperative traits in interactions both within and between species (Porter and Simms 2014).
2. *Experimental evolution*: In short-lived organisms such as microbes, experimental evolution can test theoretical predictions about, for example, the influence of spatial structure on cooperation and competition (Griffin et al. 2004). This approach has the potential also to illuminate the coevolution of two or more traits affecting cooperation within or between species.
3. *Genomics*: The rapid generation of high-quality genome sequences is already changing our understanding of the evolution of cooperation. For example, there is current debate over the relative importance of novel genes versus changes in the regulation or function of conserved genes for the evolution of eusociality in Hymenoptera (e.g., Kapheim et al. 2015). Similar questions could be asked of cooperation between species, but to date, researchers have done more to identify genes or genomic features associated with cooperation within a species than between species.

Macroevolution of cooperation

1. *Trait correlations*: Identifying life history traits that are phylogenetically correlated with cooperation within a species has shed light on the ancestral conditions under which sociality likely originated (e.g., Hughes et al. 2008; Downing et al. 2015), yet we know relatively little about traits correlated with the evolution of cooperation between species (Frederickson 2013).
2. *Evolutionary robustness*: Documenting evolutionary transitions among cooperative and noncooperative states has shown that mutualism rarely breaks down into parasitism (Sachs and Simms 2006; Sachs et al. 2011). But in social animals, how often are lineages prone to putative cheating, such as worker reproduction in social insects or “false feeding” in cooperatively breeding birds, derived from more cooperative ancestors?
3. *Lineage diversification*: The evolution of cooperation may directly affect reproductive isolation (as in pollination) or it may increase the abundance, geographic range, or niche breadth of a lineage, potentially accelerating speciation or slowing extinction. A positive correlation between interspecific cooperation and lineage diversification is supported by studies of some mutualisms (Joy 2013; Weber and Agrawal 2014). In contrast, Wilson (1992) suggested that “sociality promotes dominance but not diversity” (p. 17) in insects and mammals, but there have been few formal macroevolutionary tests of this idea (but see Cockburn 2003; Marki et al. 2015).

COMPETITION BETWEEN PARTNERS

Selection for cooperation can be undermined by competition between partners, either for the rewards of cooperation or for other limiting resources (Griffin et al. 2004; Jones et al. 2012). Competition between partners can reduce the direct benefits avail-

able from cooperation (Barker et al. 2012), and can potentially even lead to the collapse of cooperation, as illustrated by the “tragedy of the commons” (Hardin 1968). Within a species, competition occurs among partners, but in cooperation between species, competition is more common among guild members than

among partners. In cooperation between species, guild members often compete for heterospecific partners (reviewed by Jones et al. 2012), but competition between heterospecific partners for resources is rare: for example, ant queens compete for ant-plants (Frederickson 2006), but ants and plants do not compete for resources. In contrast, both competition for the rewards of cooperation and competition for other limiting resources often occur in social groups of conspecifics: for example, social amoebae compete to be among the spores and not the stalk of a multicellular “slug” of *Dictyostelium discoideum* cells (Fortunato et al. 2003), and they also compete for bacteria (i.e., food; Brock et al. 2011). Additionally, cooperation with competitors can have the indirect cost of increasing the competitive ability or number of those competitors (Taylor 1992). However, this may occur only when partners both cooperate and compete, which is far more common in cooperation within a species than between species. Thus, because of the greater overlap in resource use by conspecifics, competition is generally a more important factor in cooperation within a species than between species (Fig. 2).

In fact, competition between partners is a nearly universal feature of cooperation within a species (West et al. 2002; Frank 2003). Although the problems posed by competition can apply to cooperation among nonrelatives (e.g., West et al. 2006), they have been investigated mainly with respect to kin selection given limited dispersal (reviewed by Queller 1992; West et al. 2002). Limited dispersal increases the potential for both cooperation and competition among relatives. Notably, the benefits of kin cooperation can be exactly cancelled out by the costs of increased kin competition, when cooperation increases population density and thereby competition, but population density is regulated externally (Taylor 1992; Lehmann and Rousset 2010). Nonetheless, theory (Lehmann et al. 2008; Van Dyken 2010), and a limited amount of empirical work (e.g., Kümmerli et al. 2009b), has shown that life-cycle, dispersal, or ecological features can mitigate the competition-intensifying effect of limited dispersal and favor the evolution of cooperation in viscous populations. Stable cooperation in the face of kin competition requires that cooperation increases the local carrying capacity, thereby reducing the intensity of local competition, or that cooperation and kin competition are spatiotemporally separated (reviewed by Platt and Bever 2009). For example, cooperation could occur before dispersal, so that competition subsequently occurs with non-kin, or could be directed toward subsequent generations that do not compete with the focal individual directly, as in communal breeding (Platt and Bever 2009).

Competition between heterospecific partners is considerably rarer (Fig. 2), but can still be important for the evolution of cooperation between species. Competition between partners is likely when heterospecific cooperators occupy the same trophic level; for example, species engaged in Müllerian mimicry may overlap

in resource use (Elias et al. 2008; Fig. 2). This type of cooperation between species is rare and has received relatively little research attention (Box 1). Whether the evolution of cooperation between species that also compete for resources, such as Müllerian mimics, affects the strength of interspecific competition depends on whether cooperation changes the population densities of partners and thereby intensifies competition. Cooperation between species may also produce shared group resources that are the objects of competition, as in mixed-species group foraging by birds (Hino 1998). Theory predicts that, as for cooperation within a species, competition could disrupt selection for cooperation between species (Ranta et al. 1993). Thus, one reason that interspecific cooperation generally occurs between species in different kingdoms or domains may be because they do not compete for resources. Alternatively, distantly related species may be more likely to produce different resources, which they can then exchange to their mutual benefit; this is the subject of the next section.

RESOURCE-GENERATING EFFICIENCY

Cooperative partners may differ not only in the resources they consume, but also in the resources they are able to produce (Fig. 2). Variation in resource-generating efficiency sets the stage for partnerships where goods or services in different currencies are exchanged, analogous to economic trading by humans. Indeed, the theory of comparative advantage from economics also applies to biological trading (Noë and Hammerstein 1995; Schwartz and Hoeksema 1998): each party specializes in the goods or services that it is best at producing, and exchanges them for others generated by its trading partners. A major challenge is to determine the “exchange rates” of the different goods and services. The “currencies” of these goods or services are often different components of fitness; for example, nutrition may be exchanged for reproduction (Fig. 1). Alternatively, different subcomponents of, say, nutrition may be exchanged for each other, with the subcomponents having different relative values. For example, how much carbon should plants trade to receive a given amount of phosphorus or nitrogen? For interactions within a species, the concept of reproductive value provides a “universal currency” (Gardner et al. 2011) when a population is structured into classes of individuals that differ from each other in some way. This is conceptually the same as assigning values to exchanged goods or services, and thus is a promising starting point for a theoretical framework for the exchange rates of different fitness components (Box 1).

The conditions under which specialized resource production evolves and the subsequent exchange rates for the goods or services that are traded between species are predicted theoretically to be based on factors including the relative ease of producing resources oneself and the opportunities for partners to “negotiate” (Schwartz and Hoeksema 1998; Grman et al. 2012). Determining optimal exchange rates leads to the broader question of how the

benefits of cooperation are divided among partners. This question has received relatively little attention with regard to cooperation between species (Bergstrom and Lachmann 2003), but has been a major focus of intraspecific cooperation research, with the goal of predicting the conditions for social group formation and the extent to which breeding is shared equally among conspecific group members (reproductive skew; Reeve and Keller 2001).

A novel extension of intraspecific reproductive skew models is to investigate the effects of individuals' resource-generating efficiencies on the distribution of the benefits of cooperation among both heterospecific and conspecific partners (Box 1). A promising starting point is the "transactional" skew approach, which predicts how much reproduction dominant and subordinate group members should be willing to concede to each other in exchange for cooperation (Reeve and Shen 2006; Buston and Zink 2009). Applying this framework to the exchange of different resources would show how partners' resource-generating efficiencies determine the fraction of resource each should provide to the other. For example, models could predict the likelihood of stable cooperative exchange when it generates two distinct resources in different currencies that are both critical for fitness (which is likely in interspecific cooperation, where partners often produce complementary resources; Fig. 2) versus when fitness requires either but not both resources in the exchange (which is likely in cooperation within a species, where each partner is often capable of generating both resources in question). This approach would generate testable predictions about which partner holds the leverage in transactions over goods or services, and thus could lead to a theory of evolutionarily stable "exchange rates" for biological currencies. In sum, the issue of exchange rates applies to cooperation both within and between species, and the theoretical frameworks of transactional skew and reproductive value from cooperation within species are ripe for application to cooperation between species.

RELATIVE EVOLUTIONARY RATES

In both intra- and interspecific systems, cooperation often depends on multiple traits that may evolve at different rates. This is particularly evident between species, because different loci in each species are responsible for the production of the resources that heterospecific partners exchange or share. But even within a species, there is scope for evolutionary rates to differ between two or more traits that are important to cooperative interactions, for example when conspecifics exchange different direct benefits (e.g., "helping" for future mating opportunities or territory inheritance) that are under the control of unlinked loci (Box 1). The relative evolutionary rates of two or more traits (in the same or different species) that affect the magnitude or sign of an interaction between partners shape the evolutionary trajectory of cooperation, and are predicted to be particularly important when cooperative

partners are in conflict over some aspect of the interaction; for example, queen versus worker control of sex ratio in social insect colonies (Mehdiabadi et al. 2003).

Rapid evolutionary rates are traditionally considered advantageous. A "Red Queen" arms race is often expected when coevolution is antagonistic, and is thought to select on evolutionary rates themselves (reviewed by Ladle 1992). For example, there is empirical evidence of trait escalation in "Darwin's race" between the lengths of floral tubes and pollinators' tongues (Pauw et al. 2009). However, models suggest that slower evolutionary rates can be advantageous under certain circumstances. In theory, this "Red King" effect occurs in interactions with a "snowdrift" game structure; that is, where there is an incentive to defect if one's partner cooperates (e.g., Doebeli and Knowlton 1998; Bergstrom and Lachmann 2003). This means that if both parties defect, the faster-evolving party will be selected to cooperate, while the more slowly evolving party can continue to defect. In general, whether faster or slower evolution is favored can depend on the initial combination and number of strategies (Bergstrom and Lachmann 2003), asymmetric payoffs of such strategies, and asymmetries in the number of partners (Gokhale and Traulsen 2012). In the extreme case of endosymbionts evolving rapidly within a host, the slow-evolving host always "wins" the game, at least in theory (Frenn and Abraham 2004; Damore and Gore 2011). Although the "Red King" effect was initially modeled with cooperation between species in mind, whether it could apply to the coevolution of two (at least partially unlinked) loci that encode different strategies in a social group is a subject ripe for further research (Box 1).

The potential for evolutionary rates to differ between heterospecific partners is clear (Fig. 2), but it is also possible for different traits in conspecific partners to have asymmetric rates of evolution as long as multiple (partially) unlinked loci are involved. Heterospecific partners commonly differ in the rate of accumulation of heritable genetic variation due to differences in generation time, population size, recombination rate, or migration rate (Herre et al. 1999). Although fewer, differences also exist among traits within a species, including variation in the effect sizes and dominance of mutations, as well as positions of loci on autosomal versus sex chromosomes (Charlesworth et al. 1987). In cooperation between species, selection could also be stronger on one species because of asymmetry in the frequency of the interaction (e.g., due to different population sizes; Jones and Gomulkiewicz 2012), or in the species' degree of specialization (Vázquez and Aizen 2004) and dependence (e.g., due to outside options for obtaining the benefits of cooperation). Analogous asymmetries could occur in cooperation within a species if the strength of selection differs between population subgroups; for example, males and females (Starks and Poe 1997) or queens and workers (Beekman and Ratnieks 2003). The strength of selection on traits in both intra- and interspecific cooperation

may also differ because the outcome of the interaction is less sensitive to one of the traits (e.g., Gomulkiewicz et al. 2000) or because one trait has direct fitness effects while another has indirect fitness effects, with selection generally being less efficient for loci with indirect fitness effects (Linksvayer and Wade 2016). In sum, multiple loci encoding traits important for cooperative interactions are likely to have more asymmetrical evolutionary rates when they occur in different species, but they may still evolve at different rates even within a species, with potentially important consequences for social evolution.

ASYMMETRIC STRATEGY SETS, PAYOFFS, AND OUTSIDE OPTIONS

Finally, cooperative partners may differ in the set of behavioral strategies they can employ, those strategies' payoffs, and the extent to which partners depend on each other for the benefits of cooperation (i.e., the availability of outside options). We focus on asymmetries between each class of partner, although variation among individuals is a promising direction for future research (Box 1). In this section, we show that such asymmetries arise in both intra- and interspecific cooperation, although they may differ in type and magnitude.

Common asymmetries between partners' strategy sets and payoffs include "power" to control the interaction, and the extent to which each partner invests in cooperation by paying a short-term cost (Bshary and Bronstein 2004). Asymmetries in strategy sets and payoffs can often promote high cooperation and low conflict. It is intuitive that heterospecific partners have asymmetric strategies and payoffs due to taxon-specific differences in physiology (Fig. 2); for example, a plant's strategy set would generally differ from those of its animal and bacterial mutualistic partners (Kiers et al. 2003). However, conspecific individuals also commonly differ from each other in many respects that affect strategies and payoffs, such as age, condition, dominance rank, and resource-holding potential (Lewis 2002). Asymmetries are more likely to be flexible within species than between species, and temporal plasticity in strategies and payoffs is an important component of intraspecific cooperation; for example, a current subordinate may become a dominant later, as when subordinate social wasps help at the nest while "queuing" to inherit the breeding position (Field and Cant 2009).

Asymmetries in partners' outside options can arise in two ways. One component of outside options is the opportunity to acquire resources solitarily: if resources are cheaper to acquire oneself (e.g., opportunities for solitary breeding; Vehrencamp 1983), cooperation is less likely both within and between species. A second element of outside options is the abundance of cooperative partners; this includes the number of individuals within a given class of partners, as well as the extent to which individuals rely on a single specific class of partner or multiple classes. When part-

ners are limiting, the more limiting class has power to exert partner choice. These "market effects" can maintain cooperation in both intra- and interspecific systems (Noë et al. 1991), although it is an open question whether there are common mechanisms of partner choice across both types of systems, such as screening (Box 1). Asymmetric outside options can lead to one party contributing more than the other; more equal outside options (or no outside options) lead to more equal outcomes (Debove et al. 2015), although often accompanied by an increase in conflict (Baumard et al. 2013).

Asymmetric outside options occur between conspecific partners as well as heterospecific partners; for example, cooperatively breeding bird groups may arise when helpers have limited options for solitary breeding (Vehrencamp 1983), and many plant-pollinator interactions are characterized by asymmetric specialization (Vázquez and Aizen 2004). However, due to species-specific differences, heterospecific partners may be more likely than conspecific partners to have qualitatively different outside options (Fig. 2). Given that the availability of outside options depends on the biotic and abiotic environment (i.e., the context in which cooperation takes place), a change in the environment may thus be more likely to affect each heterospecific partner differently, whereas conspecific partners may be affected in the same way. Context-dependence has been a major focus of research on cooperation between species (Chamberlain et al. 2014; Hoeksema and Bruna 2015); for example, partnerships can become more beneficial when there are decreases in habitat quality (Thrall et al. 2007) or resource availability (Pringle et al. 2013). The analogous prediction for cooperation within a species (e.g., that helpers or workers have a more positive effect when the environment is less favorable) has not been widely tested or received consistent support (Magrath 2001; Koenig et al. 2011). Greater context-dependence in interactions between species than within species is an intriguing possibility, and a promising avenue for future research.

Synthesis

In sum, heterospecific partners differ from conspecific partners along five major independent axes that affect the evolution of cooperation (Fig. 2): (1) the possibility of sharing alleles due to common descent, (2) resource use and thus intensity of competition between partners, (3) generation of goods or services and thus the currencies in which the benefits of cooperation are given and received, (4) evolutionary rates, and (5) strategy sets and outside options. While the last four differences are generally true for most interactions—that is, asymmetries in these characteristics are frequently greater between heterospecific than conspecific partners—only point (1) is virtually always true, because heterospecifics do not share alleles by common descent, except

under unusual circumstances such as horizontal gene transfer. That said, not all cooperation within species occurs among partners that share alleles identical by descent. One implication of heterospecific partners having separate gene pools is that they are not competing with each other for fitness; instead, an individual's fitness must be compared to those of its conspecific competitors (Jones et al. 2015). A second implication is that cooperation between species does not bring kin-selected benefits in the same way that cooperation within a species does (Frank 1994; Zink 2015). However, analogous interdependence of fitness can be achieved in other ways (Frank 1994; Roberts 2005; Queller 2011).

We conclude that cooperation within and between species are not categorically different evolutionary phenomena (Figs. 1 and 2). This is because the characteristics of a given cooperative interaction depend on how partners in the interaction differ from each other. While these asymmetries between partners are often associated with interspecific differences, they are not intrinsically linked to differences between species. Indeed, most cooperation within and between species involves some asymmetry between partners (Fig. 2); asymmetries are particularly important when goods or services are exchanged (Schwartz and Hoeksema 1998), but also when shared group benefits are produced (Barker et al. 2016). The axes along which partners differ are largely orthogonal, giving rise to many possible combinations of partner asymmetries. Thus, the differences between intra- and interspecific cooperation, as well as differences between specific cases within each type of cooperation, are continuous.

Relatedness is only one of these key axes (Fig. 2). Along this axis, cooperating with an unrelated conspecific is much the same as cooperating with a heterospecific partner, because neither generates indirect fitness benefits; in fact, the term “mutualism” is sometimes applied to cooperation among non-kin (e.g., Clutton-Brock 2009). However, our contribution here is to clarify that the similarities between intra- and interspecific cooperation also depend on the other four axes in Fig. 2, specifically whether partners exchange goods or services in similar or different currencies, the degree to which partners compete for the benefits of cooperation or other resources, asymmetries in the evolutionary rates of cooperative traits, and differences in strategy sets and outside options.

Many intra- and interspecific interactions are not interchangeable because cooperative interactions between species are often underpinned by the exchange of resources a species cannot produce itself, and many of the benefits from cooperative breeding arise from helping relatives (Fig. 1). However, in other cases the specific attributes of a partner are less important and the benefits of cooperation could be achieved by interacting with a range of partner types that could be from the same or different species; for example, defense against predators, or acquiring general food items as opposed to specific nutrients. We expect these “generalized” interactions to include the types of interspe-

cific cooperation most similar to intraspecific cooperation, such as “shared-benefit mutualisms” (e.g., mixed-species foraging and Müllerian mimicry), and vice versa, such as resource exchange among non-kin conspecifics. These types of interactions have been relatively understudied, and are an exciting future research direction (Box 1). In sum, recognizing the parallel processes affecting cooperation within and between species, as well as the continuous differences between them, expands our understanding of the diversity of cooperative interactions in nature.

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