Shifts between cooperation and antagonism driven by individual variation: A systematic synthesis review

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ABSTRACT

The outcomes of ecological interactions fall along a continuum from cooperative (mutually beneficial) to antagonistic (detrimental to one or both parties). This applies at both interspecific (e.g. plant-animal interactions) and intraspecific levels (e.g. male-female interactions). Phenotypic variation among individuals is increasingly being recognised as an important factor in ecological processes, and trait variation in either interacting party may determine the outcome of the interaction, such as whether a symbiont provides net costs or benefits to their host, or whether two conspecifics decide to cooperatively forage or to compete over food. This systematic review investigates the role of intraspecific trait variation ('ITV') in determining the cooperative-antagonistic outcome of ecological interactions. Based on a literature collection of 95 empirical and theoretical publications meeting our inclusion criteria, we give an overview of the various mechanisms that can lead to shifts between antagonism and cooperation within or between species. We describe two broad classes of interrelated mechanisms that may drive shifts in outcomes. First, *trait frequency effects* occur when processes influencing a population's composition of traits linked to cooperation or antagonism (e.g. aggressive personality types, cheater/exploiter phenotypes etc.) lead to net shifts in interaction outcome. Second, *systemic variance effects* occur when changes in the amount of ITV in the population (as opposed to the mean phenotype) is the factor driving shifts. Both heritable genetic differences among individuals and phenotypic plasticity are important sources of phenotypic variation. The specific mix of heritable vs. plastic ITV may determine whether a change from cooperative to antagonistic, or vice versa, is likely to be short-term (i.e. context-dependent) or lead to more persistent shifts (e.g. mutualism breakdown). To guide future research on this topic we describe knowledge gaps and divergences between empirical and theoretical literature, further highlighting the value of applying research synthesis methods in ecology and evolution.

Key words: state-dependence, phenotypic plasticity, individualised niche, individual variation, individual, animal personality, variance, kinship, relatedness, systematic review

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I. INTRODUCTION

Intraspecific trait variation (‘ITV’) is ubiquitous across taxa and traits. Among-individual variation arises within species through a combination of underlying genetic/epigenetic variation (e.g. via mutation, selection and genetic drift), and phenotypic plasticity (e.g. via environmental effects on trait expression that vary at a population and/or individual level). So an individual’s phenotypic traits fall along spectra of heritability and plasticity (Lynch & Walsh, 1998; Bolnick *et al.*, 2003). Individual trait differences can be linked to intraspecific task specialisation and niche differentiation (Dall *et al.*, 2012), i.e. the ‘individualised niche’ (Müller *et al.*, 2020).

The degree and nature of ITV in a population can influence the strength and outcome of ecological interactions via multiple mechanisms (Bolnick *et al.*, 2011). For example, the mean across individuals of some nonlinear function of an individual trait is generally different from the function of the mean trait in the population (nonlinear averaging, Jensen’s inequality, Jensen, 1906). As a second interrelated mechanism, different responses of individuals to environmental fluctuations buffer population dynamics against strong environmental stochasticity (the portfolio effect, Tilman, Lehman, & Bristow, 1998). ITV can have direct ecological consequences that are independent of its heritability, but also more long-term implications for eco-evolutionary dynamics (Bolnick *et al.*, 2011). Most theoretical studies on the effects of ITV in ecological interactions have explored how ITV can alter the strength and stability of an interaction (as in Moran, Wong, & Thompson, 2017). For example, ITV can determine the superior competitor in an interspecific competitive interaction, and may promote or hinder their coexistence (Hart, Schreiber, & Levine, 2016; Uriarte & Menge, 2018; Milles, Dammhahn, & Grimm, 2020). However, in these models it is often assumed that, no matter what the level of variation is, the interaction stays competitive.

Here we explore whether and under what circumstances ITV can have even more drastic consequences and lead to qualitative changes in the nature of an interaction. Ecological interactions fall along a two-dimensional continuum defined both by the fitness effect of party A on party B and by the effect of party B on party A. Here we focus on changes in the quality of the interaction outcome from cooperative/mutualistic (i.e. providing beneficial outcomes to both parties) to antagonistic (i.e. detrimental to one or both parties; Bronstein, 1994) or vice versa. Note that we adopt the term *mutualism* to refer to beneficial interspecific interactions, and *cooperative* to inclusively refer to beneficial interactions at inter- and intra-specific levels (as per West *et al.*, 2007). Recent modelling and empirical evidence suggests that a balance of cooperative-antagonistic interactions within networks may be closely associated with their stability at a population and community level (Mougi & Kondoh, 2012; Montesinos-Navarro *et al.*, 2017). Furthermore, the position of an interaction along the continuum (or the cooperative-antagonistic 'quality' of the interaction) is not necessarily fixed; for example biotic and abiotic environmental factors can change the net outcome of an interaction between positive and negative (Chamberlain, Bronstein, & Rudgers, 2014). An example of such a qualitative change would be a competitive interaction turning into a cooperative one or vice versa. Movements between cooperative-antagonistic outcomes over ecological time frames appear to be relatively common (Bronstein, 1994; Chamberlain *et al.*, 2014), and may lead to long-term evolutionary transitions (e.g. 'mutualism breakdown', Sachs & Simms, 2006).

Variation between cooperation and antagonism is relevant to both interspecific and intraspecific interactions. In interspecific interactions, this may correspond to variation in *consumer-resource interactions* (including beneficial versus exploitative animal-plant interactions, e.g. Anjos *et al*., 2020*;* Morris *et al.,* 2007), variation between mutualism and competition/predation effects in *food-web interactions* (Chamberlain *et al.*, 2014), or variation between mutualistic and parasitic *host-symbiont interactions* (i.e. the mutualism-parasitism continuum; Karst *et al.*, 2008; Canestrari *et al.*, 2014). In intraspecific interactions, the cooperation-antagonism continuum may correspond to variation between cooperation and competition within *socially interacting dyads* or *groups* (Sachs *et al.*, 2004), between reproductive cooperation/ parental care and conflict in *male-female pairs* or *parent-offspring relationships* (Arnqvist & Rowe, 2005; Székely *et al.,* 2007).

How can the presence of ITV in one or both interacting partners affect shifts along cooperation-antagonism continua? The most obvious way is if there is intraspecific variation in a trait that directly influences how cooperative or antagonistic an individual acts in an interaction (e.g. cooperative vs cheater, sociable vs aggressive phenotypes). Processes influencing the composition and frequency of these traits within a population may shift the quality of an interaction between mutualism and antagonism (referred to here as *trait frequency effects*, Fig. 1A). In addition to these more straightforward effects, changes in the amount of trait variance within a population may have both direct and indirect effects on the quality of an interaction (referred to here as *systemic variance effects*, Fig. 1B). In this case the level of variation in traits may lead to changes in interaction outcomes, even where the trait may be seemingly unrelated to cooperation or antagonism. For example, the amount of among-individual variation in fecundity can affect patterns of relatedness in neighbourhoods, and therefore whether cooperation is favored (Rodrigues & Gardner, 2013). Furthermore, the direction of these effects can be counterintuitive. For example, if individuals on average act weakly mutualistically, an increase in among-individual trait variance will introduce additional antagonistic individuals, which can shift the average interaction towards stronger mutualism. This can happen, for example, because cooperative/mutualistic interactions may rely on partner choice or cheater punishment mechanisms, which stabilizes the positive interactions by selecting against antagonistic individuals, which in turn can only be maintained in the presence of some antagonistic individuals (Foster & Kokko, 2006; McNamara & Leimar, 2010).

Information on how ITV can lead to such qualitative shifts in an interaction is currently scattered in the empirical and theoretical literature and the phenomena outlined here can go by many names. Our goal was therefore to summarise and provide a conceptual synthesis of literature relating to the question: "*How can intraspecific trait variation shift an interaction along the gradient from antagonistic to mutualistic interactions, both for intraspecific and for interspecific interactions? For example, can intraspecific variation in hosts and/or parasites (individualised niches) change the relationship so that the net effect of the "parasite" on the host becomes positive?"* The literature collection for this review was obtained primarily using a systematic review to establish an unbiased cross-sectional coverage of relevant literature, supplemented with additional non-systematic articles to ensure comprehensive coverage.

II. METHODS

Search Strategy and Protocol

A systematic search was conducted using a query with terms relating to (a) cooperative/mutualistic interactions, (b) antagonistic interactions, and (c) individual ecological variation (general query: *("*mutualis*" OR "cooperati*" OR "interdependenc*" OR "symbio*") AND ("antagonis*" OR "competi*" OR ("host*" AND "parasit*") OR* *(“predator*” AND “prey”) OR “conflict”) AND (("intraspecific” OR “within-species” OR “individual*” OR “agent*” OR “organism*” OR “animal*”) NEAR/5 (“varia*” OR “divers*” OR “difference*”)))*. Searches were conducted in Web of Science (18/07/2019; refined to categories Ecology, Evolutionary Biology, Zoology and Behavioural Sciences) and Scopus (18/07/2019; refined to the subject area Agricultural and Biological Sciences; see full search strategy in Appendix S1). Records from each database were deduplicated via R package ‘revtools’ (v 0.4.1, Westgate, 2019) and manually, giving 411 unique records.

Study Selection

Titles and abstracts of each record were screened for inclusion by two reviewers (from a pool of eight) to avoid individual biases in selection, using randomised author-, journal-, and metadata-blind screening. Records were included for full-text screening where they were considered relevant, or potentially relevant, to our research question (as stated above). Conflicting decisions (140/411, 34%) were resolved by a third reviewer. Based on a preliminary assessment of each paper’s topic, full-texts were allocated to a reviewer (from a pool of 15) based on their specific expertise. 192 full-text records were screened based on the following criteria: (1) Is the paper accessible in English or German?; (2) Is there an interspecific or intraspecific interaction that can vary from cooperative/mutualistic to antagonistic?; (3) Is there trait variation?; (4) Is the trait variation intraspecific?; and, (5) Does the ITV influence the mutualistic/antagonistic direction of the interaction? Variation in the strength of a cooperative interaction without evidence of corresponding variation in antagonism, or vice versa, was not considered as a shift in the cooperative-antagonistic quality of an interaction here, i.e. there needed to be variation specific to an interaction that could show both mutualistic and antagonistic qualities. Papers not meeting all criteria were excluded. Empirical studies with humans as the focal species were also excluded as beyond the scope of the review (although theoretical or modelling studies based on humans, but with potential general applicability could be included). Initial reviewer decisions were double-checked for consistency and conflicting decisions were resolved collaboratively (by NPM, MJW, include/exclude conflicts for 16/192 papers, 8.3%).

To complement this collection and ensure comprehensive coverage of the literature, additional non-systematically sourced papers that met our criteria were also included from: (i) papers identified from the references of papers included from the above systematic searches; and (ii) relevant papers already known to authors. For included studies, we extracted at least: the type of study (empirical, observational, review, theory/modelling); the scale of ecological interaction considered (interspecific, intraspecific, both); and, the types of ecological interactions considered (host-symbiont, cooperative-competitive, male-female etc.). Review records following PRISMA reporting guidelines (Moher *et al.*, 2009), are available in online supplementary materials, Appendices S1, S2, and the Open Science Framework (https://osf.io/9kfpc/; doi: 10.17605/OSF.IO/9KFPC).

III. RESULTS

For the following narrative synthesis, we grouped our collection of studies by the scale of the interaction influenced by individual variation (interspecific, intraspecific or both), and the interaction type, identifying five broad interrelated classes of continua (Fig. 2). Trends and themes in primarily modelling/theoretical studies are then described separately. Our search identified 95 relevant papers, including 78 systematic and 17 non-systematically sourced studies (see Fig. 3). This collection was composed of experimental/observational studies (49%, 47/95), literature reviews (20%, 19/95), and modelling/theory studies (36%, 34/95; note, there is some overlap between groups). For publication trend/ bibliometric analysis and summary tables for all included studies with details of the types of the respective types of ITV and their effect on cooperation vs antagonism, see Appendices S3 and S4. The collection covers research topics and study systems ranging from interspecific plant-animal and host-symbiont interactions, to intraspecific social, female-male and parent-offspring interactions.

1. *Interspecific Interactions*

1.1. *Consumer/resource or plant/animal mutualism-antagonism continuum:*

In many interspecific interactions there is some nutrient or energetic transfer between parties, such that they may be viewed as consumer-resource interactions (Holland *et al.*, 2005). However, the resources derived, services provided and fitness effects from the interaction may be either the same or different between parties. Variation in distribution, control and competition over mutual resources, e.g., through variation in strength of exploitation, social learning, competitive ability, virulence or (partner) quality, creates a dynamic landscape of mutualistic-antagonistic interactions where any single interaction between heterospecific individuals may reside (Jones, Bronstein, & Ferrière, 2012). This dynamic quality is notable in the interactions of plants and their animal partner species. ITV in plant morphological and reproductive traits (e.g. flower and seed productivity; Cariveau *et al.*, 2004; Pesendorfer *et al.*, 2016) can alter the relative strength of an individual plant's mutualistic (e.g. pollination, seed dispersal) and antagonistic (e.g. seed predation) interactions. The net outcome for an individual plant's reproductive success (and thus the degree of mutualistic benefit of animal interactions) can also depend on its spatial position in relation to its local population, as well as the composition of the interacting partner species (Rodriguez-Rodriguez, Jordano, & Valido, 2017). Additionally, a plant's interactions with a single animal species can show mutualistic-antagonistic variation, such as *Allomerus octoarticulatus* ants that nest on and provide protective services to the leaves of *Cordia nodosa* plants, but the same ants also show intraspecific variation in their foraging behaviour, feeding on and damaging leaves (Edwards *et al.*, 2006). Potentially, the mutualistic-antagonistic outcome of an interaction may be influenced by ITV in both the animal and the plant species.

Behavioural variation may lead to various outcomes in interspecific interactions. Bottlenose dolphins (*Tursiops truncatus*) show intraspecific variation in foraging tactics, where individuals either directly compete with human fishermen or show cooperative behaviour with those fishermen (Cantor, Simões-Lopes, & Daura-Jorge, 2018). This behavioural ITV is a learned cooperative strategy that reduces both heterospecific competition and investment in searching for food, with the potential trade off of higher competition with conspecifics. Variation in heterospecific cooperativeness has also been described for complex superorganisms such as social insects, for example, colonies of nest-sharing ant species of the genera *Camponotus* and *Crematogaster* (Menzel & Blüthgen, 2010). Costs include enhanced food competition associated with aggression in fighting for shared resources, while benefits arise from common nest defence, shared foraging and brood care. Whether the interaction outcome leads to cooperative nest-sharing between *Crematogaster modiglianii* and *Camponotus rufifemur* is linked to their behavioural phenotypes, including their tendency to initiate a nest, foraging behaviour, trail following and nest defence (Menzel & Blüthgen, 2010). Whether grazing herbivores display competitive versus cooperative behaviours towards heterospecifics may be dependent on local environmental factors, where sheep (*Ovis aries*) and red deer (*Cervus elaphus*) may display avoidance behaviour at high population densities due to resource competition, and attraction/swarming behaviour towards heterospecifics at low densities as indicators of the same resources (Perez-Barberia *et al.*, 2015). Thus, the variation in mutualistic-competitive behaviour may be driven by trade-offs and variation in an individual’s abiotic and biotic environment.

Heterospecific interactions exist in a dynamic community context, where an individual's interactions with third-party species can be an environmental factor that shifts interactions between mutualism-antagonism. For example, hemi-epiphytic plants play a crucial role in nest stabilization of *C. modiglianii* and *C. rufifemur* ants, and promote mutualistic outcomes (Menzel & Blüthgen, 2010). Similarly, common reeds (*Phragmites australis*) show variation in their soil-microbial communities associated with their lineage (e.g. native vs invasive), such that interactions between reed plants and heterospecific grasses may either be inhibitory or facilitative depending on the reed's symbiotic associations (Allen *et al.*, 2018). As such, heterospecific interactions outcomes can be influenced by variation in individual behaviour or morphology as well as more cryptic variation, such as one party's interactions with third party species.

1.2. Host/symbiont mutualism-parasitism continuum:

A particular class of interspecific interactions that can show mutualistic-antagonistic variation are those between hosts and their symbionts. Among-individual variation in the genotype or phenotype of either party, often in combination with environmental conditions, can tip the balance between benefits, i.e. the symbiont-conferred fitness gain, and costs, e.g. through virulence. For example, within the parasitoid wasp *Asobara tabida*, females show genotype-linked intraspecific variation in their dependence on *Wolbachia* for oogenesis (Dedeine, Bouletreau, & Vavre, 2005). Likewise, endophytic fungi of *Abies beshanzuensis* trees show intraspecific variation in chemical defence traits (Yuan *et al.*, 2011). Based on their traits and the environmental conditions, these fungi may provide benefits for the host tree or act as parasites.

In cases where there is covariance between genetic variation and the quality of a host-symbiont interaction (as above), outcomes may be mediated by indirect third-party effects. For example, the fungus *Amylostereum areolatum* is a symbiont of siricid woodwasps (*Sirex noctilio*). This symbiont can have indirect antagonistic effects for woodwasps by providing food to mycophagous nematodes, which also parasitize and sterilize the wasp host. Fungal strains that do not support nematode development instead provide positive protective effects on hosts (Hajek, Morris, & Hendry, 2019). Similarly, pea aphids (*Acyrthosiphon pisum*) infected with facultative symbionts, *Hamiltonella defensa,* are protected from parasitism by a third-party parasitoid wasp, but aphids bear constitutive fitness costs (Vorburger, Ganesanandamoorthy, & Kwiatkowski, 2013). Certain *H. defensa* strains provide different levels of protectiveness, and are non-randomly distributed among host populations (Niepoth, Ellers, & Henry, 2018). Infection of *H. defensa* strains in their non-native host lineages can cause higher host mortality and inhibit reproduction, which might explain their limited spread in host populations.

Intrinsic factors, such as sex and ontogenetic variation in hosts, can lead to the simultaneous existence of mutualism, commensalism and parasitism in interactions between the same two species. In the cleaning symbiosis between crayfish (*Cambarus spp.*) and ectosymbiotic branchiobdellidans (*Cambarincola spp.*), the host may benefit from symbiont cleaning activity but symbionts may cause gill scarring by feeding on host tissue, e.g. in smaller crayfish, under food limitation or at high densities (Brown *et al.*, 2012; Thomas *et al.*, 2016). Similarly, the presence of a phoretic mite (*Poecilochirus carabi*) can have mutualistic, neutral and antagonistic effects on the fitness of its burying beetle host (*Nicrophorus vespilloides*), but the outcome is dependent on the sex and life stage of beetles, and the density of mites. For example, adult male’s lifespan was reduced by the presence of mites, whereas the effect on female lifespan was dependent on the size of her mate (De Gasperin & Kilner, 2015).

Behavioural ITV can influence the outcomes of host-symbiont interactions and interspecific interactions generally, leading to the formation of cheater-sanction dynamics in predominantly mutualistic relationships, such as cleaner-client fish mutualisms. Individual cleaner wrasse (*Labroides dimidiatus*) differ in the quality of service they provide to hosts and can even behave as situational exploiters, acting as an ectoparasite feeding on host tissue (Bshary & Grutter, 2002; Bshary & Schäffer, 2002). In both plant-animal and host-symbiont mutualisms, some individuals may employ a strategy that is detrimental to their partner, where 'cheater' phenotypes may receive a fitness advantage by gaining benefits from the partner species without reciprocating (Sachs, 2013; Frederickson, 2013). While this has the potential to lead to mutualism breakdown [see for example a rapid shift toward parasitism in the jellyfish symbiont *Symbiodinium microadriaticum* (Sachs & Wilcox, 2006)], cases of evolutionary breakdown of mutualisms appear relatively rare (Sachs & Simms, 2006), and control mechanisms against antagonistic individuals are also often observed. An example is behavioural variation in cleaner wrasse hosts, the longnose parrotfish (*Hipposcarus harid*), where wider ranging parrotfish can switch between cleaning sites and select more mutualistic partners. Switching may support the maintenance of net-mutualistic interactions by acting as a control mechanism against antagonistic cleaner behaviours, illustrating the roles of competition over clients and partner choice in shaping interaction outcomes (Jones *et al.*, 2012). Similar partner control mechanisms appear in plant-animal interactions, where senescence of damaged leaves appears to be a sanction against their resident ant mutualists of *Cordia nodosa* plants that damage host leaves (Edwards *et al.*, 2006). Intraspecific variation in one species (i.e. cheater-cooperator phenotypes) may therefore act in concert with an evolved selective pressure intrinsic to their mutualistic partner (i.e. sanctions), to prevent shifts towards antagonism.

2. *Intraspecific Interactions*

2.1. *Conspecific cooperation-competition continuum*

There are some key differences between cooperation/mutualism at inter- and intraspecific levels. In intraspecific interactions, cooperative outcomes may be more likely to evolve because of relatedness (i.e., sharing of alleles identical by descent) providing additionally indirect fitness benefits to cooperative individuals, while competition may be more intense due to greater phenotypic similarity between parties. Nonetheless, inter- and intraspecific interactions can both produce fitness benefits and cooperative outcomes with some key mechanistic similarities (Barker *et al.*, 2017). Variation in the resources that an individual consumes or produces (as in bottlenose dolphin-human mutualisms), as well as variation in partner choice or reward (as in cleaner wrasse-parrotfish mutualisms), similarly influence the level of intraspecific cooperation (Barker *et al.*, 2017). These forms of variation may arise within species at magnitudes comparable to interspecific differences, due to ITV in age, condition, dominance rank or resource-holding potential as well as temporal plasticity in these traits, leading to outcome variance in intraspecific interactions.

The expression of aggressive/cooperative behaviours can be driven by underlying among-individual variation, which can be genetic (Helms Cahan, 2001; Sinervo *et al.*, 2007), epigenetic (McAuliffe *et al.*, 2015), and phenotypic, and most likely a combination of these three. Phenotypic variation may include body size (Whiteman & Côté, 2004), physiology (Schoepf & Schradin, 2013; Platt, Seyfarth, & Cheney, 2016), learning and cognition (Platt *et al.*, 2016), parasite infection status (Barber *et al.*, 2017), and the social state of individuals (Roberts, 1998; Hamilton & Ligocki, 2012; Riebli *et al.*, 2012; Singh & Boomsma, 2015; Platt *et al.*, 2016). These factors can affect the expressions of individual aggressive-cooperative phenotypes, which appears to be a key form of ITV that determines the qualitative outcomes of interactions with conspecifics (i.e. have a *trait frequency effect*). For example, seed-harvester ant (*Messor pergandei*) foundresses may form cooperative multi-female nests or monogynous colonies, as determined by their aggressive-sociable responses, where each ant's response is determined by a combination of underlying genetic variation and behavioural plasticity driven by the phenotype of the other female (Helms Cahan, 2001; Helms & Helms Cahan, 2012).

Partner identity is an important determining factor, where the direct and indirect fitness benefits for the individual appears to be critical. Following conflicts, long-tailed macaques (*Macaca fascicularis*) are more likely to reconcile with conspecifics that they perceive to be of high value in terms of gaining resources (Cords & Thurnheer, 1993). Genetic similarity is key in the cnidarian *Hydractinia symbiolongicarpus*, where "cooperation" (as in colony fusion) is determined genetically: colonies sharing allorecognition alleles will fuse, whereas colonies not sharing any allele will engage in conflict (Nicotra *et al.*, 2009). Similarly, in social yellow-bellied marmot groups (*Marmota flaviventer*), affiliative interactions appear to be structured around the kin relationships between individuals, their age, and their individual social state (Wey & Blumstein, 2010; Wey, Jordán, & Blumstein, 2019).

State-dependent variation in cooperation may occur in response to differences in ecological conditions (e.g. rainfall effects on helping behaviour in cooperatively breeding banded mongooses, *Mungos mungo*; Marshall *et al.*, 2016), ontogenetic variation (e.g. age-dependent coalition formation in barbary macaque, *Macaca sylvanus*; Rathke *et al.*, 2017), body condition (e.g. condition-dependent helper responsiveness in *M. mungo*; Bell, 2008), and/or future fitness expectations (e.g. helping behaviour in wasps such as *Polistes dominulus* and *Liostenogaster flavolineata*, Field & Cant, 2006). Similarly, for cooperatively breeding groups, the expression of various cooperative behavioural traits (e.g. offspring provisioning, brood care, territorial defence, nest construction, etc.) may vary intraspecifically due to various factors, including age, gene expression, body size and morphology (Komdeur, 2006). Group size may be particularly important; for example, studies in non-human primates suggest that when the group size of interacting conspecifics increases, smaller sub-groups may be more likely to form (Sih, Hanser, & McHugh, 2009). Individuals will then behave cooperatively with sub-group members, but the proportion of competitive relationships will increase across the larger network.

Studies found evidence for individual physiological, i.e. hormonal, mechanisms that play a key role in mediation of inter-individual interactions (Komdeur, 2006). Platt *et al.* (2016) found that oxytocin levels affect cognition in rhesus macaques (*Macaca mulatta*), which in turn affects decisions to behave cooperatively or competitively. Conversely, another study on the Southern hairy-nosed wombat (*Lasiorhinus latifrons*) did not find a relationship between hormone profiles and decision-making (Walker, Taylor, & Sunnucks, 2007); instead the cooperative-competitive outcome was determined by a state-dependent response to their physical environment. A similar pattern was found in capuchins (*Cebus apella*), where decisions to cooperate were context-dependent, but not influenced by exogenous oxytocin (Smith *et al.*, 2019), suggesting that the relationship between individual physiology, behavioural strategy and environmental factors are likely to be species-specific. Interaction outcomes can also influence the hormonal state of individuals, as in the African striped mouse (*Rhabdomys pumilio*). Solitary individuals have a significantly lower corticosterone level compared to mice living in groups, which suggests that individuals adopt a solitary tactic to avoid reproductive competition and social stress from group-living (Schoepf & Schradin, 2013). This suggests potential feedbacks between physiological state and conspecific interaction outcomes.

Exploitation of predominantly cooperative social networks (i.e. cheating) also occurs in intraspecific interactions, analogous to exploiter/cheater phenotypes in interspecific interactions. These cheater phenotypes represent a shift towards antagonism within populations, but often occur only at low frequencies because of negative frequency-dependent selection (Kraemer & Velicer, 2014), or other costs associated with the cheating (Aukema & Raffa, 2004). Control mechanisms include policing, e.g. aggressive behaviour towards conspecifics as a punishment for mediating fitness losses due to competition (Singh & Boomsma, 2015). This phenomenon appears usually when there is lack of reciprocity (Roberts, 1998), and aims to mediate conflicts while favouring cooperation. In social insects for example, the more efficient policing is, the more cooperation (i.e. less selfish egg-laying by workers) is observed (Wenseleers & Ratnieks, 2006). So depending on the degree of policing in a species (or the composition of policing phenotypes within a population), factors that introduce more antagonistic individuals into a cooperative society may be buffered against.

2.2. Female/male cooperation-conflict continuum

Studies included here on female-male interactions are mostly centered around parental care, often in birds where cooperative behaviour may include shared brood care and nest defence (Schuppe, Sanin, & Fuxjager, 2016), and imbalances between parties in care or partner desertion represent antagonistic outcomes. Participation in parental care is costly and individual condition can be an important factor, as in the common murre (*Uria aalge*), where decisions to take turns in nest care and foraging to feed offspring is condition-dependent (Takahashi *et al.*, 2017). In the penduline tit (*Remiz pendulinus*), increased male attractiveness and physical condition shift the balance of male-female care away from cooperation (van Dijk *et al.*, 2010, 2012). This suggests an individual’s expectations regarding their future fitness (i.e. their residual reproductive value) may be a key factor in an individual's parental care investment. The Kentish plover (*Charadrius* *alexandrinus*) shows a comparable pattern where the ability of a parent to find a new mate is linked with their likelihood of desertion, in which mate-finding ability appears to favor female desertion in this species (Székely, Thomas, & Cuthill, 2006). Although one may expect this to be sensitive to fluctuations in population sex ratio and individual attractiveness.

Similar to other interaction types, abiotic or biotic environmental conditions also appear to drive variation in cooperative parental care. A long-term data set on helping effort in cooperative breeding of banded mongoose groups found that rainfall levels influenced helping behaviour of males. Male sex-biased survival under poor conditions, notably low rainfall, led to older males participating more in helping behaviour (Marshall *et al.*, 2016). In burrowing beetles (*Nicrophorus vespilloides*), within-family interactions are affected by the presence of mites, through sex dependent fitness costs. Males paid a high survival cost when mites were present, whereas for females this was dependent on the size of the male, where females paired with smaller males had a longer survival, altering the fitness costs and benefits from parental care (De Gasperin & Kilner, 2015).

ITV in endocrinological or neuronal networks is a factor underpinning parental care behaviours, which can be both state-dependent and show longer-term variation among individuals (Trillmich, 2010). For example, male African striped mice (*R. pumilio*) display highly divergent reproductive strategies that are associated with different levels of hormones (e.g. prolactin, testosterone), which can be linked to the expression of parental care and intraspecific conflict behaviours (Schradin *et al.*, 2009). While it appears that the quality of male-female interactions can be sensitive to environmental factors, we found only relatively few studies that explicitly considered the role of ITV in these interactions and how the quality of those interactions may shift.

Few papers in our literature collection considered sexual conflict over mating decisions and mostly considered the two extremes, i.e. coercive versus cooperative strategies. Hence, we know less about whether intraspecific shifts occur, or what traits might be involved. One example is described in the pea leafminer (*Liriomyza huidobrensis*), where males can employ a highly cooperative dancing courtship strategy, or a more direct and possibly coercive strategy (Ge *et al.*, 2019). As males are reliant on female ovipositor punctures in leaves for food, hungrier males are more likely to use a dancing courtship strategy as this produces more ovipositor punctures. This strategy also improved longevity and fecundity in females, so represents a shift to a more cooperative mating strategy. Patterns in intraspecific sexual conflict, reproductive skew and female choice across species might give a hint at the ecological and individual variation that could be involved (Bro-Jørgensen, 2010; Surbeck *et al.,* 2017), and could provide a framework to also consider the role of ITV in coercive-cooperative mating variation.

2.3. Parent/offspring care-conflict continuum

Parent-offspring interactions may also show variation between conflict and care, and following from the above examples, decisions to not contribute to parental care can also reflect a more or less caring parent-offspring interaction. This will occur where one parent provides a relatively lower level of care alone, so non-participation by one parent will be detrimental to offspring development (although this is not always the case, see Székely *et al*., 2006). The parent-offspring continuum could be considered to extend beyond direct parents to changes in participation in cooperatively breeding groups (Trillmich, 2010), as in the banded mongoose example above where the degree of care provided by adults towards offspring of the group varied with the adult's hunger, body condition and sex (Marshall *et al.*, 2016). Individual state and environmental factors are similarly expected to influence this level of parental and alloparental care provided to offspring, and be subject to policing in group contexts (Komdeur, 2006; Trillmich, 2010).

3. *Modelling ITV along cooperation-antagonism continua*

Numerous theoretical models relate to how intraspecific variation can influence positions on cooperation-antagonism continua (see Table S3, Appendix S4), addressing a range of interaction types, traits, and mechanisms which may shift interaction outcomes. Notably, studies consider effects on within- and between-species interactions, as well as evolutionary transitions from single- to multicellular organisms, as there are strong mechanistic parallels between cooperative-antagonistic shifts across scales (Michod, 1997). At each scale, a shift toward cooperative interactions requires that the direct and indirect fitness benefits of cooperation are balanced against the interests of an individual unit of selection, i.e. an individual cell or organism. So despite the majority of modelling studies focusing on intraspecific interactions, they are likely to have some mutual relevance across levels, although with some key differences, e.g. a greater role of genetic relatedness and shared alleles between interacting parties in intraspecific (and intercellular) scales, as well as a greater likelihood of phenotypic similarity between parties (Barker *et al.*, 2017). Finally, it is worth noting that although much of the theory in this section remains abstract, some work has been inspired by, or linked with, the behaviour of specific species (e.g., Sinervo *et al.*, 2007 on lizards, Van Dijk *et al.*, 2012 on penduline tits).

3.1. *Kin selection*

Relatedness between interacting individuals and the resulting inclusive-fitness effects play an important role in many studies on cooperative-competitive shifts in intraspecific interactions. Hamilton (1964) provides a theory of inclusive fitness, known as kin selection, showing that it is best to help another individual (i.e., cooperate) if $rb > c$, where r is relatedness, b is the benefit to the other individual and *c* is the cost to oneself. This is known as Hamilton's rule and provides a gene-eye perspective on whom to cooperate with. There may be different levels of relatedness among pairs or groups of individuals, in the cues or signals that indicate relatedness (both in transmission and reception abilities), and in perceived (or real) differences in costs and benefits of actions; so Hamilton's rule provides numerous theoretical routes into this topic. There are strong but complex relationships between relatedness and ITV. On the one hand, relatedness with interacting individuals can be seen as a biotic environmental factor that varies among individuals and that may cause them to behave more or less cooperatively. On the other hand, relatedness among individuals in a group or population is also related to its level of phenotypic variation, simply because more related individuals will exhibit more similar traits. Simultaneously, the degree of group relatedness affects the willingness of group members to contribute to offspring-rearing in collective breeding groups (Savage *et al*., 2013). The precise effect depends on the specific relatedness, such as those between helpers and offspring, or helpers and dominant individuals.

Kin selection is also relevant to the social evolution of herd defences. As more individuals in a group develop defences, predators or pathogens become less likely to attack any individual in the group. Frank (1998) finds that the higher the relatedness between individuals, the higher the chance that individuals induce such defences, due to inclusive fitness, so cooperation increases with increasing relatedness. If individuals differ in the amount of resources they obtain, they will strongly diverge in how much defence they will induce, but the average amount of defence is not affected. That is, the shift between cooperation and competition is at the individual level, where the degree of variation within groups (i.e. the level of relatedness or variation in resource use) can have an indirect effect on the interaction outcome.

High relatedness promoting cooperation can also be generated by variation in other traits. For example, variation in fecundity can increase relatedness within neighbourhoods, and thus promote cooperation (Rodrigues & Gardner, 2013). More generally, variation in fecundity can either promote helping or harming, depending on the spatial structure of the environment and whether or not individuals can help high-quality individuals (Rodrigues & Gardner, 2013). These can be considered indirect *systemic variance effects*, where changes in the level of variation within a population lead to a state-dependent change in the expression of cooperative or antagonistic behaviours.

3.2. Social discrimination

Variation in a phenotypic trait can serve as the basis for social discrimination (as tags) and thus the formation of groups where individuals cooperate within the group but not with outsiders. Hochberg *et al.* (2003) provide a model showing that when social discrimination evolves, it causes phenotypically similar individuals to form into different, spatially distinct groups. The formation of stable groups only occurs for altruistic and selfish interactions, but not for spiteful and mutualistic interactions. Similarly, cooperation or antagonism may in some circumstances depend on cultural traits. In a simple form, this may be an arbitrary trait that defines the cooperative social group ('in-group favoritism'), or provides the possessor with prestige ('prestige hierarchy') (Ihara, 2011). In Ihara (2011), the emergence of cultural traits is considered in a gene-culture coevolutionary model, identifying the conditions under which such traits lead to the formation of discriminate social interactions (i.e. stable cooperative groups/hierarchies), in the context of intraspecific competitive social interactions.

3.3. Effects of information and noise

One of the key benefits of cooperation is gaining information about what to do in particular circumstances. For example, information is critical for ‘policing’ one’s partners if they display antagonistic ‘cheater’ phenotypes. The iterated prisoner’s dilemma is a game that is often used to study cooperation, where there is an immediate short-term benefit of not cooperating (defecting) in any given round, but where choosing not to cooperate can lead to others not cooperating (or interacting) in the future. Uncertainty about the strategies of others can determine whether it is best to cooperate. For instance, if there is considerable variation (e.g., due to mutation) in the number of rounds before defection in the iterated prisoner's dilemma, it can make sense for individuals to cooperate for longer than the population average and cooperativeness increases in the population (McNamara, Barta, & Houston, 2004; Barta, 2016). In some cases, the effect of noise on cooperation can be subtle. For example, Ito *et al.* (2017) consider the evolution of a trait which governs the investment in an interaction, with variation in interactions coming about through noise (i.e., individuals making errors). They find that the magnitude of errors does not influence the emergent strategy, but that the magnitude influences convergence stability.

3.4. Variation in intraspecific competitive ability and resource acquisition

In many studies, variation in competitive ability between individuals influences whether individuals cooperate, e.g. in foraging situations, or behave antagonistically. Ranta *et al.* (1993) use an information-sharing model to analyse how phenotypic variation may influence decisions to forage in conspecific groups (based on three-spined sticklebacks, *Gasterosteus aculeatus*). Where a phenotype is related to how likely an individual is to get a share of food in group foraging scenarios, cooperative foraging becomes detrimental to lower ranked individuals. This suggests that cooperative behaviour be more likely in phenotypically similar groups. Indeed, three-spined sticklebacks appear to prefer schooling with similar-sized individuals (e.g. Ranta, Lindström, & Peuhkuri, 1992), but better protection against predators in more homogeneous schools might also contribute. Furthermore, genetic variation in traits related to competitive ability, e.g. body size, can lead to indirect genetic effects, e.g. when larger individuals behave aggressively towards smaller individuals, thereby further increasing the differences in body size. Such indirect genetic effects can lead to coevolution of variation in traits such as body growth rate and competitiveness and cooperativeness (Marjanovic *et al.*, 2018), and thus potential shifts along the cooperation-antagonism continuum.

Whether variation in competitive ability promotes or hinders cooperation can be context-dependent (as found in empirical studies). In a producer-scrounger game, the frequency of producing i.e. finding new food patches (versus scrounging, i.e. exploiting food patches found by others) can be seen as variation between cooperation and antagonism. Lee *et al.* (2016) find that variation in competitive ability affects the proportion of scroungers (i.e. shift the population along the cooperation-antagonism continuum) and the direction of the effect depends on resource availability. If resources are scarce, the scrounging frequency goes down with increasing variation in competitive ability, because only the most competitive individuals have a chance to scrounge the few encountered food patches. But if resources are plenty, scrounging frequency goes up with increasing variation in competitive ability because more individuals have the chance to take advantage of the large number of encountered food patches. This could also be considered a *systemic variance effect* on interaction quality.

In fighting situations, costly displays can be seen as cooperative because they help resolve the fight and reduce its costs. Such displays can only evolve if there is sufficient variation in strength (i.e. ability to win contests) (McNamara & Leimar, 2010). Thus, the level of among-individual variance in strength may have systemic effects on the quality of intraspecific cooperation-conflict interactions. Interestingly, the effect of ITV in fighting ability can also go in the other direction. Franz *et al.* (2011) consider a situation where individuals with access to a resource may either share it mutually (e.g., through turn-taking) or engage in an antagonistic conflict (i.e., fight over it). They construct a model where there is non-heritable variation in fighting ability and find that over a range of parameter values, there are alternative stable states (turn-taking and competition). They find that the turn-taking strategy becomes more stable when interacting individuals are less able to identify the stronger individual. Thus, by making it more obvious who is strongest, increasing ITV in strength should hinder the evolution of cooperative turn-taking.

Also variation in resource acquisition among individuals in a group can drive differences in cooperative behavior. For example, cooperative food sharing can emerge if resource acquisition varies between individuals but also over time within an individual's life (Barta, 2016). Dubois & Giraldeau (2003) provide models of iterated decisions, based on a modified hawk-dove game. They identify that 'cooperative' behaviour should occur when food supplies sufficiently outweigh would-be competitors, and those that are efficient in finding new food will 'cooperate' more easily than those that rarely find food first. When resources vary, a cooperative group may require a level of policing to prevent individuals taking advantage of others. Frank (1996) looks at the evolution of policing in a population that is subdivided into groups. When relatedness is high, individuals self-restrain to reduce overall competition. At low relatedness, this does not happen and instead policing emerges, where individuals invest some resources into decreasing overall competition for their group. When resources vary across individuals, those with more resources invest more into policing, to maintain cooperation. In both of these studies, the shift between antagonism and mutualism appears to happen on the individual level, with those individuals receiving more resources behaving more cooperatively. Liu *et al.* (2020), using game theoretic modelling similarly finds that individuals that are more capable of acquiring resources invest more in cooperative behaviors than subordinate individuals. Furthermore, this is sensitive to resource supply, where under harsher environmental conditions (i.e. reduced resources), the relative investment of subordinate individuals in cooperative behaviours is increased (which was further demonstrated experimentally in burying beetles, *Nicrophorus nepalensis*).

Similar to variation in competitive ability, variation in male quality or attractiveness can also drive shifts between conflict and cooperation in male-female interactions. The larger variation in male quality, the more repeatable is male mate finding success, and the less willing are males to invest in raising individual broods (Lehtonen & Kokko, 2012).

3.5. Stabilization of cooperation by variation in partner quality

Variation in partner quality can promote the evolution of choosiness, which penalizes less cooperative individuals and thus promotes cooperation. This mechanism can operate at multiple levels. First, it can promote the evolution of cooperation among individuals within a population (McNamara & Leimar, 2010). As in the intraspecific case, interdependence between variation in partner quality and the evolution of choosiness can lead to mutualism-antagonism shifts also in interspecific interactions. Song & Feldman (2013) consider the coevolution of variation in plant reward systems and animal choosiness in plant-animal mutualisms, such as in pollination and seed dispersal. For trait variation in reward systems in plants to evolve, animals must be choosy about which plants they visit, which leads to the plants evolving higher rewards (more mutualistic). However, if this process proceeds for a long time, the variation in plants will be purged and hence the choosiness in the animals will break down. As a consequence, animals do not need to be choosy any more. If the trait variation in plants is (partially) non-heritable, it cannot be purged and choosiness in the animals will be maintained. Similarly, Foster & Kokko (2006) studied a host-symbiont model and found that sufficient standing genetic variation in symbiont quality is required to maintain host choice and stabilise the mutualism. This was also considered in the context of cleaner-client fish interactions, where the relative abundance of exploitative phenotypes and victims, produced variation in the level of partner control in a game-theoretical model (Johnstone & Bshary, 2008). Analogous to cheater or exploiter phenotypes in inter- and intraspecific interactions, the emergence of antagonistic defector cells (e.g. through mutation) and control mechanisms appear to stabilise higher-level units of organization (Michod and Roze, 2001; Michod and Nedelcu, 2003; see also Rainey and Kerr, 2010).

3.6. Direct benefits of variation among interacting individuals

In pairs or groups of interacting individuals, variation among the interacting individuals can sometimes provide direct benefits, i.e. give rise to a cooperative/mutualistic interaction. Such benefits of variation among interaction partners have been termed “social heterosis” by Nonacs & Kapheim (2007). As a specific example, Uitdehaag (2011) studies a system where individuals differ in how their resource acquisition is affected by environmental fluctuations. On their own they would suffer from variance discount, i.e. variation in number of offspring leads to a reduction in long-term fitness. Uitdehaag (2011) proposes that fitness can be buffered if individuals engage in a mutualism with partners that are very different from them, so they perform well in different conditions and hence can support each other at different times. Thus, such mutualisms would only emerge when there is sufficient intraspecific variation in environmental responses. Barta (2016) discusses that a predisposition for specialization can promote the evolution of cooperation. For example, differences between males and females in the types of parental care they can provide best can promote the evolution of cooperative parental care. Similarly, a leadership hierarchy within a group may make the group more efficient than another, though this may be counterbalanced by the battle over leadership within the group, resulting in a tension between absolute fitness of individuals across groups and relative fitness of individuals within groups (Hamilton, 2013; Pinter-Wollman *et al.*, 2016).

In the context of interdependencies between interacting microbial strains or species, Estrela *et al.* (2016) considered how variation among partners in the benefits they provide each other influences interaction outcomes. The formation of functionally mutually interdependent interactions was most likely where there were intermediate levels of ‘leaky’ traits (i.e. the level that the benefits of a function are isolated to the organism performing the function), where high privatization of function leads to independent genotypes and low privatization lead to some exploitation. This suggests that the formation of stable mutualisms is sensitive to the degree of benefit each party provides.

3.7. Shifts in intraspecific interactions mediated by other species

Warning signals are typically regarded as cooperative traits within a species because individuals benefit from other individuals “educating” predators about their toxicity. However, often individuals in a population differ in their toxicity (perhaps due to environmental heterogeneity). Speed & Franks (2014) show that such variation in signals can lead to antagonistic interactions within the population where less-defended individuals are trying to look more like well-defended individuals and thus exploit them. Well-defended individuals, on the other hand, are trying to look as different as possible from the less-defended ones. Although predators are involved, this represents a shift in a cooperative-competitive intraspecific interaction. In host-parasite systems, Stopka & Johnson (2012) identify that the variance in parasite loads causes different levels of need for help through allogrooming (i.e., resulting in different payoffs for the same amount of help). Thus intraspecific variation altered the game dynamics and the resulting modified game was more conducive to cooperation. This appears to be an environmentally mediated state-dependent shift, where variation here is non-heritable.

IV. DISCUSSION

For a long time, ITV was considered as noise around an optimum value, but variation both between and within individuals is increasingly recognised as an important factor influencing various ecological processes (Bolnick *et al.*, 2003, 2011; Dall *et al.*, 2012; Violle *et al.*, 2012; Westneat, Wright, & Dingemanse, 2015). Our review builds on this work by investigating the role that ITV plays in determining the outcome of interactions along cooperative-antagonistic continua. In this context, it is important to consider that the level and characteristics of ITV in a population are not constant, but may be influenced by processes that affect its genetic composition and diversity, as well as individual variation in phenotypic plasticity (i.e. reaction norms, Nussey, Wilson, & Brommer, 2007; Dingemanse *et al.*, 2010). For example, mutation and migration/invasion may be sources of ITV and introduce rare antagonistic phenotypes in predominantly mutualistic partner species (as suggested in both Foster & Kokko, 2006; Frederickson, 2013). Furthermore, selective pressure can influence levels of ITV either directly, through selection on traits linked to interaction quality, or indirectly through evolutionary trade-offs (Wolf & Weissing, 2010). Additionally, phenotypic plasticity may also be a source of ITV, either where there is environmental variation at an individual level, and/or where individuals vary in their response to the environment (e.g. exposure of cryptic genetic variation under extreme conditions, Paaby & Rockman, 2014; or trait canalization under optimal conditions, Careau, Buttemer, & Buchanan, 2014). Environmental effects can alter levels of both between- and within-individual variation, through bet-hedging strategies or sub-optimal performance

(Wolf & Weissing, 2010). Thus, many factors influence the degree of ITV within a population and how stable that variation is over time, which will have implications for the stability (or fluidity) of interaction outcomes.

Covariation between a trait and the cooperative-antagonistic outcome of an interaction was evident in several included empirical studies (e.g. Sinervo *et al.*, 2007; Cantor *et al.*, 2018). Where there is trait-outcome covariance, selective pressures acting on among-individual trait variation -- or state-/context-dependent expression of that trait (within-individual trait variation) -- may alter the quality of the average interaction across a population. These *trait frequency effects* (as in Fig. 1A) are the most direct way that ITV can facilitate a shift in the quality of cooperative-antagonistic interactions within ecological timeframes. Trait-specific selective pressures may occur due to extrinsic factors (e.g. predation pressure, Aukema and Raffa, 2004), or factors intrinsic to the interacting parties (e.g. cheater punishment mechanisms as antagonistic-trait specific selective pressure, Edwards *et al.*, 2006; Jones, Bronstein, & Ferrière, 2012). Individual behavioural variation appears to play a large role in interaction outcomes at an interspecific (Menzel & Blüthgen, 2010; Cantor *et al.*, 2018) and intraspecific level (Sinervo *et al.*, 2007; Schoepf & Schradin, 2013). Consistent among-individual variation in personality is common (e.g. aggression, sociality, boldness), and this variation can also be subject to selective pressures through personality effects on reproduction and survival, although patterns are likely to be species-specific (Smith & Blumstein, 2008; Trillmich, Müller, & Müller, 2018). Similarly, there may be geographic variation in traits associated with interaction strength and outcome in interspecific mutualisms (Dedeine *et al.*, 2005; Helms & Helms Cahan, 2012), so demographic shifts in populations, e.g. due to trait-specific immigration/emigration, are a potential source of *trait frequency effects*.

State- or context-specific expression of cooperative-antagonistic traits also appears common. Whether an individual displays a cooperative or antagonistic behavioural phenotype in an interaction may be related to innumerable state variables (i.e. any element of an individual's extrinsic or intrinsic environment that is strategically relevant to their future fitness, Wolf & Weissing, 2010). In intraspecific interactions, there were many examples of state-dependent cooperativeness (e.g. due to body size or parasite infection status, Whiteman & Côté, 2004; Barber *et al.*, 2017), including examples of strategic adaptive expression of cooperative phenotypes (e.g. strategic reconciliation behaviour in long-tailed macaques, or habitat-specific group burrowing in hairy nosed-wombats, Cords & Thurnheer, 1993; Walker, Taylor, & Sunnucks, 2007). State-dependent cooperation was also evident in parent-parent/ parent-offspring interactions (Trillmich, 2010; van Dijk *et al.*, 2010, 2012; Marshall *et al.*, 2016), as well as in interspecific interactions (Menzel & Blüthgen, 2010; Perez-Barberia *et al.*, 2015). That the outcome of any interaction may be conditional or context-dependent has long been recognised (Bronstein, 1994), and does not necessarily rely on behavioural variation (see for example the context-dependency of siricid woodwasps interactions with symbiotic fungi, Hajek, Morris, & Hendry, 2019). Whether these lead to long-term changes in an interaction, and have potential evolutionary implications, may depend largely on the nature of the state factor involved, e.g. if state differences among individuals are labile or stable over time (Wolf & Weissing, 2010).

These mechanisms are also playing a role in *systemic variance effects* (as in Fig. 1B), i.e. where the level of variance in a population influences the outcome of interactions. For example, in social discrimination and kin selection contexts (Hamilton, 1964; Hochberg *et al.*, 2003), greater among-individual variation is expected to increase competitive interactions with conspecifics, due to reduced indirect fitness benefits for the individual. This manifests through state-dependent expression of cooperative-competitive behaviour at the individual-level, where the average individual would behave less cooperatively in a high ITV population. Additionally, increased phenotypic variance in partners may introduce antagonistic individuals to a predominantly cooperative population (e.g. cheaters in interspecific mutualisms, Frederickson, 2013), and intraspecific contexts (cheaters/exploiters in intraspecific cooperative interactions, Aukema & Raffa, 2004). This may induce the expression of cheater punishment traits (e.g. selective abortion of oviposited fig fruits that receive poor pollinations service, Frederickson, 2013; policing behaviours in eusocial insects, Singh & Boomsma, 2015), which acts as an antagonistic-trait-specific selection pressure. These cases of *systemic variance effects* appear to induce phenotypic plasticity responses (i.e. within-individual trait variation), that enhance individual fitness outcomes and/or maintain stable cooperative-mutualistic interactions.

The level and nature of ITV involved is likely to influence the nature of cooperative-antagonistic shifts and the time scale on which they happen. Factors that influence the level of ITV in a population (e.g. mutation, immigration, demographic shifts, individual plasticity variation etc.) can shift an interaction along cooperative-antagonistic continua by affecting the amount of variation in traits related to *systemic variance effects*. Additionally, the degree of plasticity in a trait, and its costs, may influence how readily *trait frequency effects* occur. Both *systemic variance effects* and *trait frequency effects* can occur on the time scale of an individual life span if traits are plastic or state-dependent, or on a longer evolutionary time scale spanning multiple generations if ITV is linked to heritable genetic variation. For example, state-dependent changes in behavioural phenotypes may occur rapidly (e.g. variation in sheep and deer's swarming-repulsing behaviour in response to density, Perez-Barberia *et al.*, 2015), but intraspecific behavioural variation can also be highly consistent over time and heritable (Bergmüller, Schürch, & Hamilton, 2010) [e.g. variation between dolphin foraging behaviour (per Cantor, Simões-Lopes, & Daura-Jorge, 2018), which may be maternally transmitted to offspring (Whitehead, 2017)]. Moreso, expressing phenotypic plasticity and maintaining the capacity to express phenotypic plasticity (e.g. cognitive traits) may involve costs such as energetic and fitness costs, which impose limits on plastic responses (Dewitt & Scheiner, 2004). Furthermore, the degree to which ITV is linked to heritable genetic variation may determine the long term consequences of *trait frequency effects*. Where traits that determine interaction outcome are closely linked to an allele (e.g. allorecognition traits in hydrozoan *H. symbiolongicarpus*, Nicotra *et al.*, 2009), changes in allele frequency in the population will have intergenerational effects on the level of cooperation-antagonism. In extreme (and apparently rare) cases, selective pressure on heritable traits can lead to evolutionary consequences, e.g. breakdown in mutualistic relationships (Sachs, 2013). Therefore, the nature of ITV involved in an interaction is likely to influence whether any shift occurs, the persistence of that shift, and its long-term implications.

In our narrative overview of papers relating to cooperation-antagonism variation, some factors and mechanisms were prominent in both the empirical and theoretical studies in our literature collection, for example the degree of relatedness between interacting individuals. Similarly, theory suggests that intraspecific variation in mutualist quality is important for the maintenance of host-symbiont mutualistic interactions at the population level, because this variation produces selection pressures for partner choice, where partner choice in response to mutualist variation is supported by empirical evidence. On the other hand, for parent-offspring and male-female interactions, where shifts between antagonism and cooperation might also be expected, neither empirical nor theoretical publications provided much evidence or discussion of such shifts, or consideration of partner controls.

There were also clear differences in the material covered by the empirical and theoretical publications in our literature collection. Among the empirical studies, we found comparable numbers of papers for intraspecific vs. interspecific interactions (see Appendix S3, Fig. S3), but the vast majority of the theoretical papers in our data set concerns intraspecific interactions. An interesting mechanism among the empirical papers that did not appear in any of the theoretical papers includes shifts between interspecific competition or cooperation (e.g. dolphins and fishermen, ants). Another striking difference was that many of the theoretical papers but few of the empirical papers represent *systemic variance effects* at the population level (Fig. 1B). For example, some of the theoretical papers suggest that trait differences can serve as a tag for social discrimination and thereby promote cooperation or provide information on competitiveness and fighting ability. Some of the theoretical papers also concern direct benefits of variation among interacting individuals, a mechanism that did not appear among the empirical papers. Many empirical papers, on the other hand, focus on the effect of ITV in determining whether the interaction of an individual with its interaction partners, for example an individual plant and an associated animal species, is antagonistic or cooperative. Such trait shifts at the individual level may then lead to *trait frequency effects* on interaction outcomes (Fig. 1A).

Are the differences in coverage between shifts in different biological situations and for different biological mechanisms biologically meaningful or do they rather represent differences in the amount of attention given to certain phenomena or biases in our analysis pipeline? We speculate that it is probably a mixture. For example, the shortage of empirical papers reporting *systemic variance effects* may be because of the additional burden of conducting experiments at the population level. And what about the difference between empirical vs. theoretical publications? Theoretical studies of interspecific interactions usually focus on a single type of interaction, e.g. consumer-resource, and are not flexible enough to allow for shifts to a mutually beneficial scenario. Also, the types of phenomena most often reported in the empirical literature (shifts due to different traits at the individual level) are probably too straightforward to be of interest from a theoretical perspective, and if such studies exist, they might not have mentioned intraspecific variation and may therefore not be included in our data set.

The differences in literature coverage between empirical research and theory lead to some interesting suggestions for future research. Although logistically challenging, future experiments that manipulate the amount of intraspecific variation and track shifts at the population level and/or at an evolutionary time scale (e.g. in experimental evolution studies with short-lived organisms) would be extremely valuable. Such experiments could test predictions by some of the theoretical papers in our data set, e.g. whether variation in fecundity among individuals promotes cooperation by increasing relatedness (Rodrigues & Gardner, 2013). On the theoretical side, we suggest that it would be valuable to build models that allow shifts along the antagonism-cooperation axis to emerge more mechanistically from the underlying biological processes, taking into account costs and benefits at the individual level. For example, models for plant-animal interactions could take into account multiple processes (e.g. herbivory and pollination) and study how intraspecific variation in one or both partners affects the quality of the interaction.

V. CONCLUSIONS

(1) Considering movement on cooperation-antagonism continua from an individual perspective is valuable, as phenotypic variation among individuals is a key component of mechanisms that lead to shifts in the qualitative outcomes of interactions in ecological timeframes.

(2) There are a diverse range of traits involved, and the level and nature of the ITV involved (particularly trait plasticity and heritability) are likely to influence interaction-outcome variance over short term ecological time frames, as well as the long-term evolutionary implications.

(3) This general topic has been the subject of many empirical and modelling studies, but there are understudied and under-considered effects in both areas.

(4) Promoting greater integration of empirical research and theory into this topic, by applying research synthesis techniques, is valuable in informing future research in both areas.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Search strategy and information sources.

Appendix S2. Study selection.

Appendix S3. Publication trends and bibliometric analysis.

Appendix S4. Included studies summary information.

Figure Legends:

Fig. 1. Conceptual diagram showing changes in the cooperative-antagonistic quality of an interaction. Each box represents a population and its current composition of individuals/traits. Shifts occurs due to (A) *trait frequency effects*, i.e. where there are changes to the composition of phenotypes within populations, and those phenotypes are directly related to the cooperative or antagonistic outcome of interactions, and (B) *systemic variance effects*, i.e. where changes in the level of variance in a trait that is not explicitly linked to cooperation or antagonism leads to shifts between cooperative and antagonistic outcomes. Critically, a *systemic variance effect* manifests by stimulating a *trait frequency effect*. Trait value refers to an arbitrary measure of a hypothetical trait that varies between individuals within a population, and may be directly or indirectly related to cooperative-antagonistic interaction outcomes.

Fig. 2. Conceptual diagram showing interaction types and continua focused on in this review at both the interspecific and intraspecific level, the types of organisms that constitute the parties to each interaction type, and examples of traits that influence the quality of interactions .

Fig. 3. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) diagram for included studies in systematic review.

Figure 1.

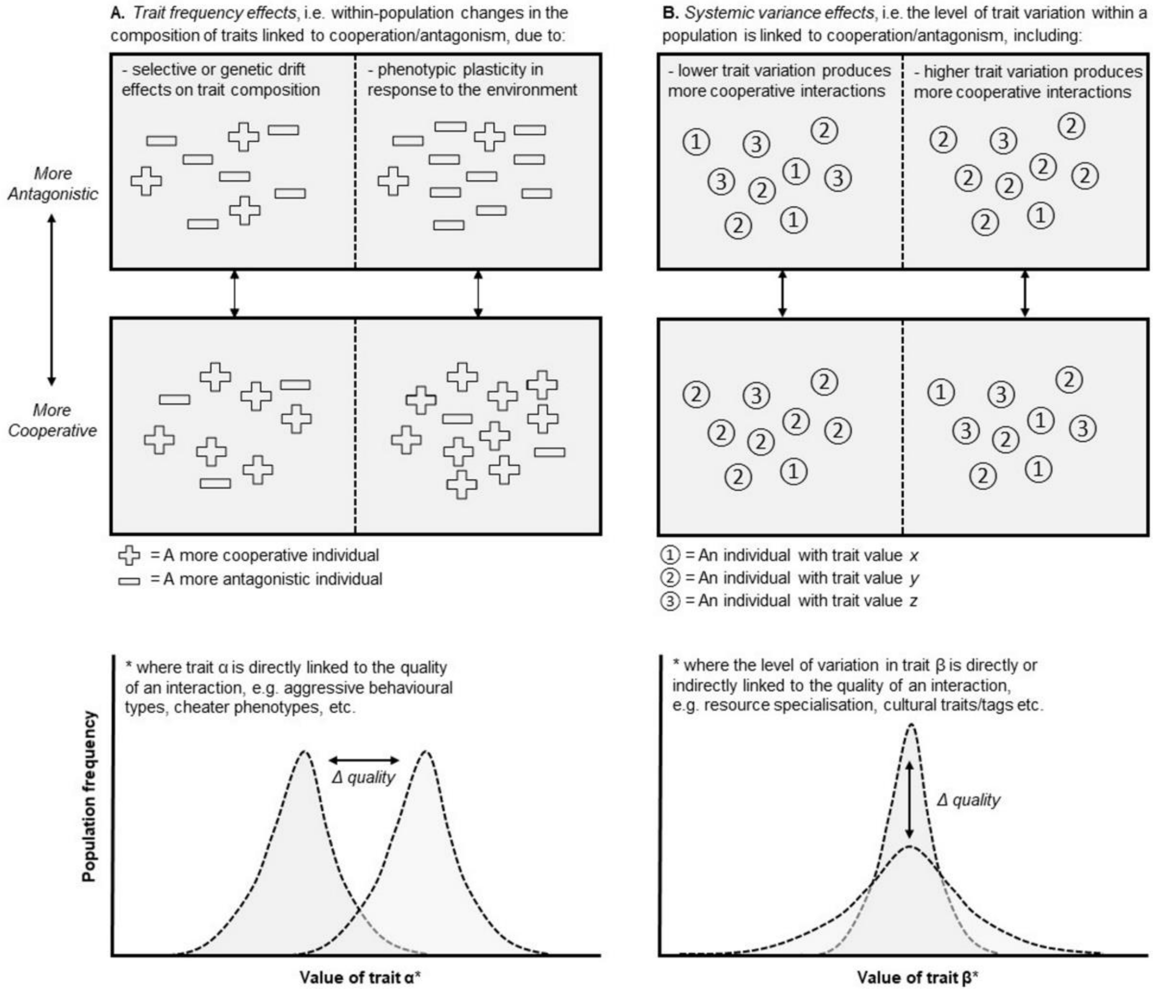
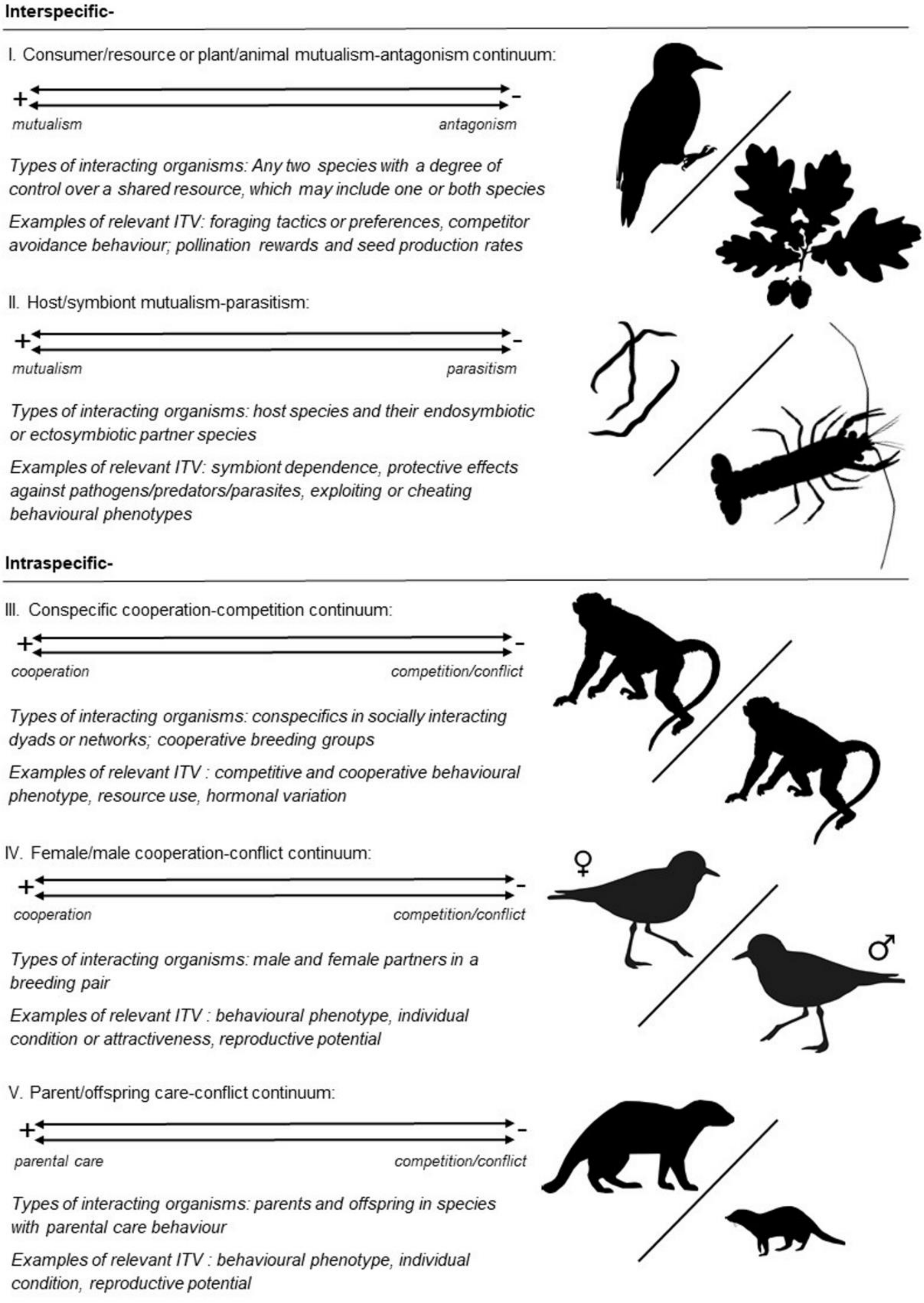

A. Trait frequency effects, i.e. within-population changes in the composition of traits linked to cooperation/antagonism, due to:
- selective or genetic drift effects on trait composition
- phenotypic plasticity in response to the environment
More Antagonistic
More Cooperative
= A more cooperative individual
= A more antagonistic individual
B. Systemic variance effects, i.e. the level of trait variation within a population is linked to cooperation/antagonism, including:
- lower trait variation produces more cooperative interactions
- higher trait variation produces more cooperative interactions
① = An individual with trait value x
② = An individual with trait value y
③ = An individual with trait value z
* where trait α is directly linked to the quality of an interaction, e.g. aggressive behavioural types, cheater phenotypes, etc.
Population frequency
Δ quality
Value of trait α*
* where the level of variation in trait β is directly or indirectly linked to the quality of an interaction, e.g. resource specialisation, cultural traits/tags etc.
Δ quality
Value of trait β*

Figure 2.



Interspecific-

I. Consumer/resource or plant/animal mutualism-antagonism continuum:

Types of interacting organisms: Any two species with a degree of control over a shared resource, which may include one or both species

Examples of relevant ITV: foraging tactics or preferences, competitor avoidance behaviour; pollination rewards and seed production rates

II. Host/symbiont mutualism-parasitism:

Types of interacting organisms: host species and their endosymbiotic or ectosymbiotic partner species

Examples of relevant ITV: symbiont dependence, protective effects against pathogens/predators/parasites, exploiting or cheating behavioural phenotypes

Intraspecific-

III. Conspecific cooperation-competition continuum:

Types of interacting organisms: conspecifics in socially interacting dyads or networks; cooperative breeding groups

Examples of relevant ITV : competitive and cooperative behavioural phenotype, resource use, hormonal variation

IV. Female/male cooperation-conflict continuum:

Types of interacting organisms: male and female partners in a breeding pair

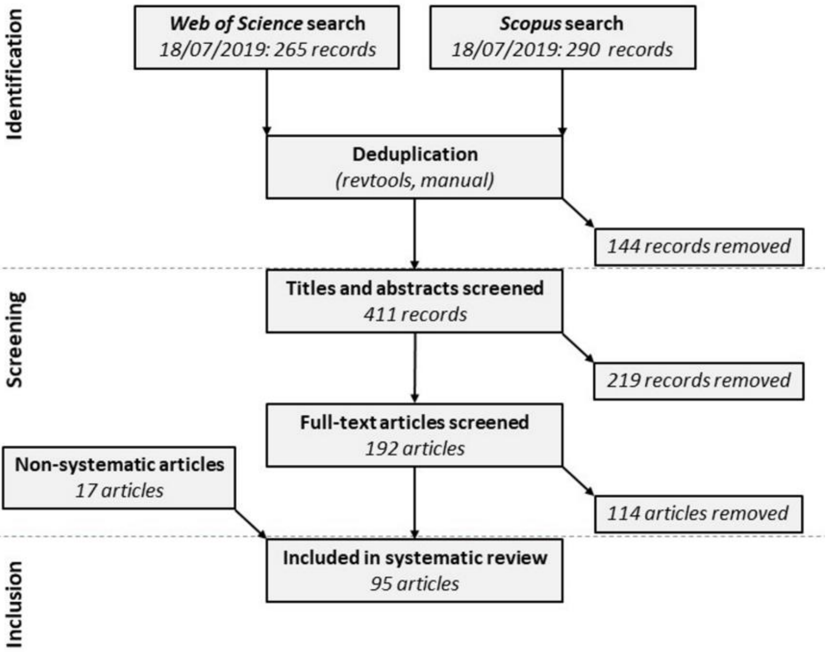
Examples of relevant ITV : behavioural phenotype, individual condition or attractiveness, reproductive potential

V. Parent/offspring care-conflict continuum:

Types of interacting organisms: parents and offspring in species with parental care behaviour

Examples of relevant ITV : behavioural phenotype, individual condition, reproductive potential

Figure 3.


Identification
Web of Science search
18/07/2019: 265 records
Scopus search
18/07/2019: 290 records
Deduplication
(revtools, manual)
144 records removed
Screening
Titles and abstracts screened
411 records
219 records removed
Full-text articles screened
192 articles
114 articles removed
Non-systematic articles
17 articles
Inclusion
Included in systematic review
95 articles