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

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Short Running Title: Shifts along cooperation-antagonism continua

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ABSTRACT

The outcomes of ecological interactions fall along continua from cooperative (mutually beneficial) to antagonistic (detrimental to one or both parties). This applies to interactions both between species (e.g. plant-animal) and within species (e.g. female-male). The outcome of an interaction, for example whether a symbiont provides net costs or benefits to its host, or whether two conspecifics cooperatively forage or to compete for food, is often not fixed. In this systematic review, we investigate the role of intraspecific trait variation ('ITV') in one or both interacting parties in determining the cooperative-antagonistic outcome of inter- and intraspecific ecological interactions. Based on a literature collection of 96 empirical and theoretical publications meeting our inclusion criteria, we give an overview of the types of interaction continua involved; traits related to outcome variance; and mechanisms as well as constraints on shifts in interactions outcomes. We propose that ITV can lead to shifts in interaction outcome via two interrelated mechanisms. First, *trait frequency effects* occur when processes influence a population's composition of traits linked to cooperation or antagonism (e.g. aggressive personality types, cheater phenotypes etc.), leading to net shifts in interaction outcomes. Second, *systemic variance effects* occur when a change in the level of ITV within populations (as opposed to the mean trait) is driving shifts in outcome. Heritable trait differences and phenotypic plasticity are sources of phenotypic variation among individuals, and both the degree of heritability and plasticity of the trait involved may determine whether shifts between cooperation and antagonism are likely to be short-term (i.e. context-dependent) or lead to more persistent shifts (e.g. mutualism breakdown). To guide future research we describe knowledge gaps and divergences between empirical and theoretical literature, highlighting the value of applying evidence synthesis methods in ecology and evolution.

Keywords: state-dependence, phenotypic plasticity, individualised niche, kinship, mutualism, personality

I. INTRODUCTION

Intraspecific trait variation (‘ITV’) is ubiquitous. Variation among individuals within a species arises through a combination of underlying genetic/epigenetic variation (e.g. via mutation, selection and genetic drift), and phenotypic plasticity (i.e. environmental effects on trait expression, where both the environmental factor driving the response and the response itself may vary at an individual level, Dewitt and Scheiner 2004). Thus, an individual’s phenotypic traits fall along spectra of heritability and plasticity (Lynch and 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 level of ITV in a population can influence the outcome of ecological interactions via multiple mechanisms (Bolnick et al. 2011). For example, through nonlinear averaging, the realised strength of an interaction in the presence of variation may differ from the strength predicted based on the mean trait (Jensen’s inequality, Jensen 1906). Similarly, different responses of individuals to environmental fluctuations buffer population dynamics against strong environmental stochasticity (the portfolio effect, Tilman et al. 1998). ITV can have direct ecological consequences that are independent of trait heritability, and also more long-term implications for eco-evolutionary dynamics (Bolnick et al. 2011). Theoretical studies of ITV effects of ecological interactions have previously explored how ITV can alter the strength and stability of an interaction (see Moran et al. 2017). For example, ITV can determine the superior competitor in an interspecific competitive interaction, and may promote or hinder species coexistence (Hart et al. 2016, Uriarte and Menge 2018, Milles et al. 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 outcome 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. We focus on cases where at least one of these mutual effects changes sign and changes the quality of the interactions 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).

The position of any interaction along the continuum (or the cooperative-antagonistic 'quality' of the interaction) is not fixed; for example biotic and abiotic environmental factors can change the net outcome of an interaction between positive and negative (e.g. 'context-dependent outcomes', as per Chamberlain et al. 2014; 'interaction norms', Thompson 1988). This outcome variance is relevant to interspecific interactions, including beneficial versus exploitative *animal-plant interactions* (Anjos et al. 2020, Morris et al. 2007), mutualistic versus competitive/predatory *animal-animal interactions* (Holland et al. 2005), or mutualistic versus parasitic *host-symbiont interactions* (Karst et al. 2008, Canestrari et al. 2014). This is also relevant to intraspecific interactions, such as variation between cooperation and competition within *socially interacting dyads* or *groups* (Sachs et al. 2004), between reproductive cooperation and conflict in *female-male pairs* or *parent-offspring relationships* (Arnqvist and Rowe 2005, Székely et al. 2007).

Variation in interaction outcomes may occur between individuals of the same species or over time (e.g. within-individual variation), which provides the material through which the net interaction quality for a species or population may change over time (e.g. 'evolution of interactions', Thompson 1988), potentially leading to longer-term evolutionary transitions (e.g. 'mutualism breakdown', Sachs and Simms 2006). Furthermore, shifts between cooperative-antagonistic outcomes appear to be relatively common over ecological time frames (Bronstein 1994; Chamberlain et al. 2014). These processes are essential to our understanding of ecological networks, as the balance of cooperation-antagonism within interaction networks may be closely associated with population and community stability (Mougi and Kondoh 2012, Montesinos-Navarro et al. 2017).

We propose that ITV in one or both interaction partners can affect shifts along cooperation-antagonism continua via two types of process. The most direct way is if there is intraspecific variation in a trait that directly influences how cooperatively or antagonistically an individual acts in an interaction (i.e. trait-outcome covariation, such as in cooperative vs cheater phenotypes). Processes influencing the composition and frequency of these traits within a population may shift the net quality of an interaction between mutualism and antagonism (referred to here as *trait frequency effects*, Fig. 1A). In addition to these more straightforward processes, changes in the level of ITV 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 a trait may lead to changes in outcome, even where the trait may be seemingly unrelated to cooperation or antagonism. For example, the level of among-individual variation in fecundity can affect patterns of relatedness in neighbourhoods, and therefore whether cooperation is favoured (Rodrigues and Gardner 2013).

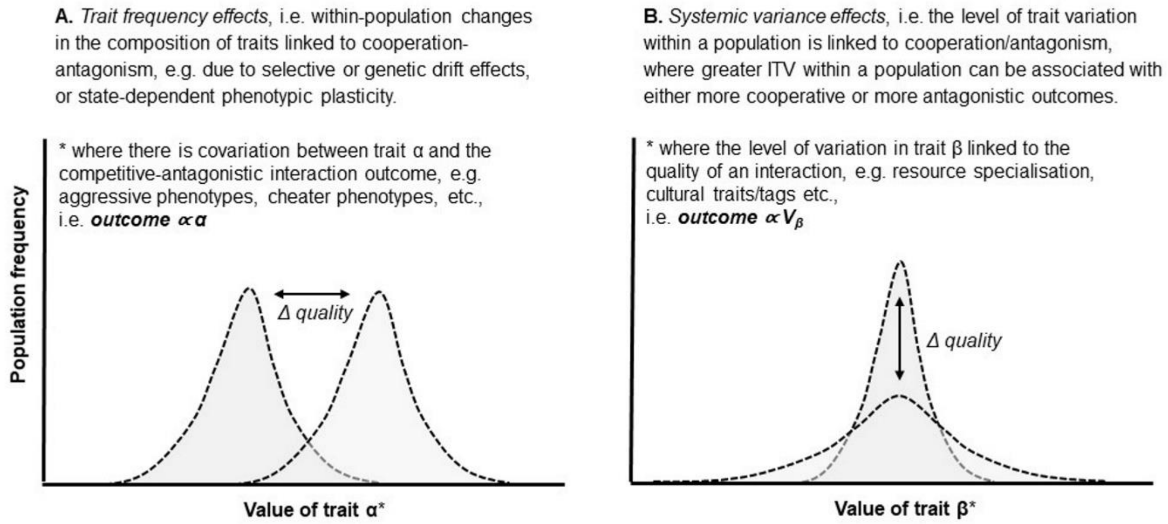


Fig. 1. Conceptual diagram showing changes in the cooperative-antagonistic quality of an interaction due to (A) *trait frequency effects*, and (B) *systemic variance effects*. Trait values (*α, β)* refer to an arbitrary measure of a hypothetical trait that varies within a population, while *Δ quality*, represents a change in the qualitative outcome of an interaction along a cooperative-antagonistic continuum.

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 a priori defined research 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?"* This review is based on a literature collection obtained primarily using a systematic literature search to establish an unbiased cross-sectional coverage of relevant studies, supplemented with additional non-systematic articles to ensure comprehensive coverage.

II. LITERATURE COLLECTION

Search Strategy and Protocol

Our systematic search used a query composed of terms relating to (a) cooperative/mutualistic interactions, (b) antagonistic interactions, and (c) intraspecific 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). Duplicates were removed via R package 'revtools' (v0.4.1, Westgate 2019) and manually, giving 411 unique records.

Study Selection

Titles and abstracts of records were screened by two reviewers (from a pool of eight) to avoid individual selection biases, using randomised author-, journal-, and metadata-blind screening. Records were included for full-text screening when considered relevant, or potentially relevant, to our predefined research question (as stated above). Conflicting decisions (140/411, 34%) were resolved by a third reviewer. Following a preliminary assessment of each paper's topic, full-texts were allocated to a reviewer (from a pool of 15) based on their expertise. 192 full-text records were screened based on the 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 cooperative-antagonistic quality, i.e. there needed to be outcome variation in 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/modelling studies based on humans, but with potential general applicability could be included). Full-text 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, non-systematically sourced papers meeting our criteria were also included from: (i) papers identified from the references of papers from the above systematic searches; and (ii) relevant papers already known to authors. For included studies, we extracted at least: the study type (empirical, observational, review, theory/modelling); the scale of ecological interaction considered (interspecific, intraspecific, both); and, the type of ecological interactions considered (host-symbiont, cooperative-competitive, female-male etc.). Review records following PRISMA guidelines are available in supplementary materials (Appendices S1-S2) and the Open Science Framework (https://osf.io/9kfpc/; doi: 10.17605/OSF.IO/9KFPC; Moher et al. 2009).

Our search identified 96 relevant papers, including 78 systematic and 18 non-systematically sourced studies (Fig. 2). This was composed of experimental/observational studies (49%, 47/96), literature reviews (21%, 20/96), and modelling/theory studies (35%, 34/96; note, there is some overlap between groups). For bibliometric/publication trend analysis and summary tables of these studies, including details of the traits/interaction types considered and effects on cooperation-antagonism, see Appendices S3 and S4. The following section provides a narrative overview and synthesis of these papers, where we describe major themes and patterns across empirical and theoretical studies from an ITV perspective. This includes: the types of interaction continua involved; traits related to outcome variance across all types of interaction; and mechanisms as well as constraints on shifts in interaction outcomes.

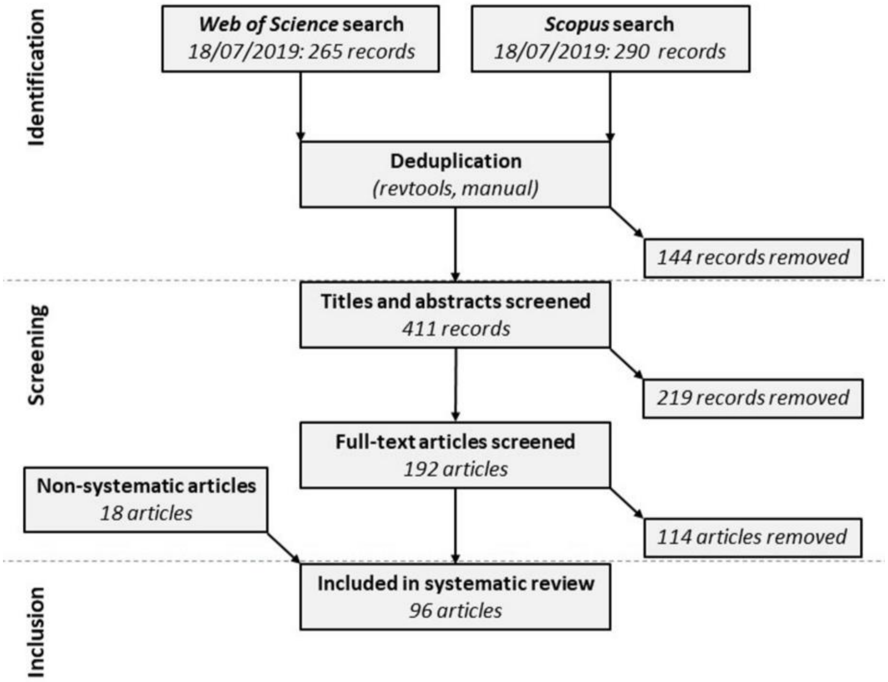


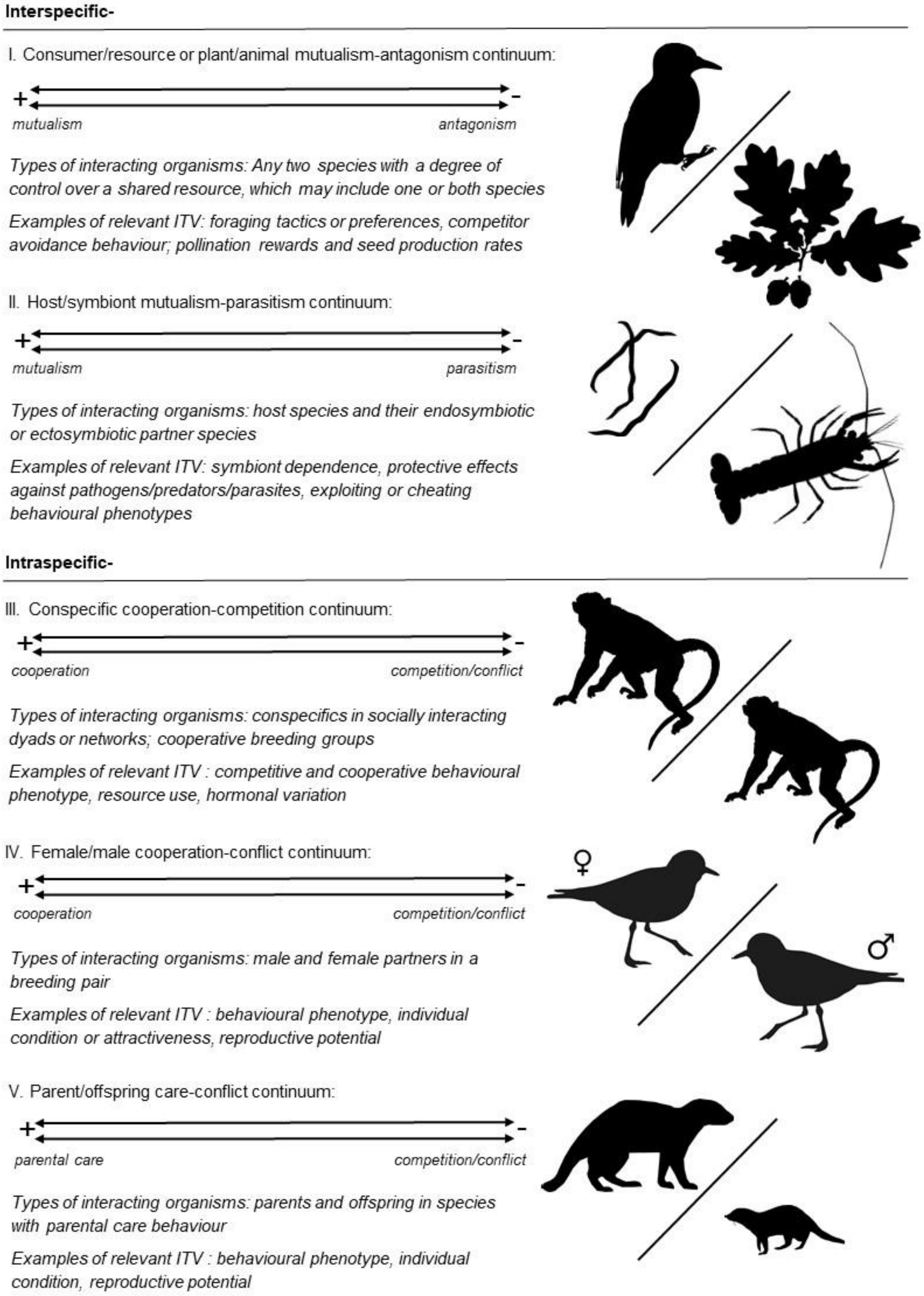
Fig. 2. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) diagram of included studies.

III. MOVEMENT ALONG COOPERATION-ANTAGONISM CONTINUA

Types and scales of continua

Studies in our collection considered interaction types ranging from interspecific plant-animal and host-symbiont interactions, to intraspecific social and parent-offspring relationships (Fig. 3). Interspecific interactions often involve some exchange of resources and/or services (i.e. consumer-resource interactions, Holland et al. 2005), where the actual costs and benefits of an interaction depend on the distribution and control of and competition for mutual resources, producing a dynamic landscape of mutualistic-antagonistic interactions (Jones et al. 2012). Outcome variation is found in plant-animal interactions, closely linked to the level of mutualistic services (e.g. pollination, seed dispersal, protection) or antagonistic effects from animal partners (e.g. destructive or exploitative feeding; Pesendorfer et al. 2016, Rodriguez-Rodriguez et al. 2017). Plant-plant interactions may also vary from inhibitory to facilitative (e.g. Allen et al. 2018), and animal-animal interactions may be competitive or cooperative in relation to food resources (Cantor et al. 2018, Perez-Barberia et al. 2015) or other shared resources (e.g. nesting sites, Menzel and Blüthgen 2010). Host-symbiont interactions are a particular form of interspecific interaction where the balance of benefits, e.g. symbiont-conferred fitness gain, and costs, e.g. virulence, may determine outcomes. This may include animal/fungal/bacterial endo- and ectosymbionts (Brown et al. 2012, Vorburger et al. 2013, Hajek et al. 2019), or physically independent symbionts (e.g. cleaner-client fish; Bshary and Grutter 2002),

Qualitative outcome variation also appears in multiple intraspecific contexts, e.g. in social groups or dyads and between parents and offspring. Socially interacting animals may display cooperation and competition over foraging (Cords and Thurnheer 1993) or breeding (Marshall et al. 2016). Cooperation in female-male interactions is often centered around parental care (e.g. brood care, nest defence in birds, Schuppe et al. 2016), and imbalances in care provision or partner desertion can represent antagonistic outcomes. A parent’s decision not to contribute to parental care is also antagonistic towards offspring where it is detrimental to offspring development (although this is not always the case, see Székely et al. 2006). The parent-offspring continuum may additionally extend to cooperatively breeding groups (Trillmich 2010), where non-parent adults care for offspring (e.g. Marshall et al. 2016).



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 continuum:

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

Fig. 3. 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 some examples of traits that influence the quality of interaction outcomes.

There are key differences and similarities between inter- and intraspecific interaction scales. Cooperative outcomes may be more likely to evolve in intra- rather than interspecific interactions because of relatedness (i.e., through inclusive fitness), but competition may also be more intense between conspecifics than between heterospecifics due to the greater phenotypic similarity and resource requirements of participants (Barker et al. 2017). Nonetheless, interactions at each scale can produce mutual fitness benefits and thus cooperative outcomes with key mechanistic similarities. For example, asymmetries in resource use and production between parties influence the likelihood and benefits of inter- and intraspecific cooperation alike (Barker et al. 2017), and variation in resource use and specialization is common within species at magnitudes that may, in cases, be comparable to interspecific differences (Bolnick et al. 2003). Additionally, shifts toward cooperation at all hierarchical scales require that the direct and indirect fitness benefits of cooperation be balanced against the interests of individual units of selection, as highlighted in theoretical studies on evolutionary transitions from single- to multicellular organisms, where a unit may be an individual cell or an individual organism (Michod 1997). So despite most modelling studies focusing on intraspecific interactions (see Appendix S3, Fig. S3), the mechanisms and processes they highlight are expected to have some mutual relevance across scales.

Covariance of traits and interaction outcomes

There are many empirical examples of apparent covariation between traits and outcomes of interspecific interactions, where the sex, age, or individual genotype or phenotype of either interaction participant may be linked to outcome variation (Thompson 1988). For example, morphological and reproductive traits in plants (e.g. flower and seed productivity; Cariveau et al. 2004; Pesendorfer et al. 2016) can alter the relative strength of mutualistic and antagonistic interactions with animals. Behavioural traits are often related to the outcomes of interactions involving animals; for example Bottlenose dolphins (*Tursiops truncatus*) display divergent foraging tactics where individuals either cooperate or directly compete with human fishermen (Cantor et al. 2018). This is a learned cooperative behaviour that reduces interspecific competition and investment in food searching, at the potential cost of higher intraspecific competition. Outcome variation has also been described for complex superorganisms, for example, colonies of nest-sharing ants *Crematogaster modiglianii* and *Camponotus rufifemur* (Menzel and Blüthgen 2010). Costs of cooperation include enhanced food competition, while benefits include common nest defence, shared foraging and brood care. Whether an interaction is cooperative or antagonistic is linked to the behavioural phenotypes of the colonies, including their tendency to initiate a nest, foraging behaviour, trail following and nest defence (Menzel and Blüthgen 2010).

Outcomes in host-symbiont interactions may be linked to genotypic variation (e.g. oogenesis-dependence on *Wolbachia* in parasitoid wasps, Dedeine et al. 2005; chemical defence traits in endophytic fungi strains, Yuan et al. 2011), and ontogenic variation (e.g. host sex and life-stage dependent effects of *Poecilochirus carabi* mites, De Gasperin and Kilner 2015). Also, either host or symbiont trait variation may influence outcomes, as in the symbiosis between crayfish (*Cambarus* spp.) and gill-cleaning ectosymbiotic branchiobdellidans (*Cambarincola* spp.). The interaction may be mutualistic, commensal or parasitic depending on the age/size of host, as well as variation in the feeding behaviour of symbionts that can cause gill scarring (Thomas et al. 2016).

For socially interacting conspecific animals, cooperation-antagonism is often associated with behavioural phenotypes (e.g. participation in group foraging, offspring provisioning, territorial defence, intraspecific aggression). Among-individual differences in cooperative-antagonistic behavioural traits may be consistent over time and underpinned by genetic or epigenetic variation, or due to state-dependent phenotypic plasticity (Helms Cahan 2001, Komdeur, 2006, Sinervo et al. 2007, McAuliffe et al. 2015). State factors that can drive the expression in cooperative-antagonistic behaviours include body size (Whiteman and Côté 2004), physiology (Schoepf and Schradin 2013, Platt et al. 2016), learning and cognition (Platt et al. 2016), parasite infection status (Barber et al. 2017), and the social state of individuals (Roberts 1998, Hamilton and Ligocki 2012, Riebli et al. 2012, Singh and Boomsma, 2015, Platt et al. 2016). For example, seed-harvester ant (*Messor pergandei*) foundresses may form cooperative multi-female nests or monogynous colonies, as determined by their aggressive-sociable phenotype, where each ant's response is determined by a combination of genetics and phenotypic plasticity in response to other females (Helms Cahan 2001, Helms and Helms Cahan 2012).

Behaviour is also key to the outcome of female-male and parent-offspring interactions, where the expression of cooperative behaviours often depends on an individual's state (e.g. condition-dependent turn taking in nest care/food provisioning in common murre, *Uria aalge,* Takahashi et al. 2017). An individual's future fitness expectations (i.e. their residual reproductive value) appears to be a key factor, where higher attractiveness, mate-finding ability and physical condition may lead to lower parental care investment and a higher likelihood of desertion (e.g. in male penduline tits *Remiz pendulinus*, van Dijk et al. 2010, 2012; and female Kentish plover, *Charadrius alexandrinus*, Székely et al. 2006). Few studies considered variation in other behaviours relating to female-male interactions, e.g. mating behaviours. One exception is the pea leafminer (*Liriomyza huidobrensis*), where males may use a highly cooperative dancing courtship strategy that improves female longevity and fecundity, or a more direct and possibly coercive strategy (Ge et al. 2019). Male courtship strategy is determined by their hunger-state as female ovipositor punctures are also a food source. Patterns in intraspecific sexual conflict, reproductive skew and female choice across species (see Bro-Jørgensen 2010; Surbeck et al. 2017) could provide a framework to also consider outcome variance in mating interactions.

Physiological (i.e. hormonal) mechanisms can play a role in intraspecific social and female-male interactions, which can be both state-dependent and show longer-term variation among individuals (Komdeur, 2006, Trillmich 2010). For example, oxytocin levels affect decisions to behave cooperatively or competitively by influencing cognition in rhesus macaques (*Macaca mulatta*, Platt et al. 2016), highlighting that hormones may be important drivers shaping the individualised niche (Müller et al. 2020). H exogenous oxytocin in capuchins (*Cebus apella*, Smith et al. 2019) were unrelated to cooperative behaviour, suggesting that relationships between hormonal mechanisms and cooperation-competition are species-specific. The reverse may also occur, with interaction outcomes influencing the hormonal state of individuals, as in the African striped mouse (*Rhabdomys pumilio*). Here, males experimentally made to live a solitary as opposed to social reproductive lifestyle had reduced corticosterone and elevated testosterone levels compared to group-living mice (Schoepf and Schradin 2013). Hormone levels (e.g. prolactin, testosterone) can also be linked to the expression of parental care and intraspecific conflict behaviours (Schradin et al. 2009), highlighting potential feedbacks between physiological state and interactions.

Trait frequency effects

This covariance between traits and interaction outcomes suggests that *trait frequency effects* (see Fig. 1A) can drive net changes in interaction quality along cooperation-antagonism continua (Thompson 1988), for example through phenotypic plasticity in cooperation-antagonism linked traits. Plasticity in interspecific mutualistic-antagonistic behaviour may be driven by local environmental factors, such as population densities (e.g. attraction-repulsion behaviour in grazing herbivores, Perez-Barberia et al. 2015). In crayfish-branchiobdellida cleaning symbioses, damaging host-tissue feeding behaviour is promoted by high symbiont densities and food limitation (Brown et al. 2012, Thomas et al. 2016), highlighting resource use and availability as potential factors driving plasticity in mutualistic-antagonistic behaviours.

Interactions with third-party species can also be an environmental factor that indirectly shifts interspecific interactions between mutualism and antagonism. In the cooperative nest sharing of *C. modiglianii* and *C. rufifemur* ants, hemi-epiphytic plants play a crucial role in nest stabilization and promoting cooperative behaviours (Menzel and Blüthgen 2010). This is a form of conditional or context-dependent outcome (*sensu* Bronstein 1994), driven by phenotypic plasticity. Similar context-dependent outcomes mediated by third-party effects are also found in some host-symbiont interactions, particularly when symbionts provide protective/defensive effects (e.g. *Sirex noctilio* woodwasp - *Amylostereum areolatum* fungal symbiont interactions mediated by the mycophagous nematodes, Hajek et al. 2019; *Acyrthosiphon pisum* - *Hamiltonella defensa* bacterial symbiont interactions mediated by parasitoid wasps, Vorburger et al. 2013, Niepoth et al. 2018).

Also for intraspecific interactions, environmental factors may drive state-dependent plasticity in cooperative-competitive behaviour. For example, Southern hairy-nosed wombats (*Lasiorhinus latifrons*) behave more cooperatively and more readily share warrens in physical environments with harder soils (Walker et al. 2007). As above, environmental factors may also include indirect third party effects, where intraspecific cooperativeness may be influenced by parasite loads (Stopka and Johnson 2012, Barber et al. 2017), or predator-prey interactions (Speed and Franks 2014). Environmental effects on parental and alloparental care are also expected (Komdeur, 2006, Trillmich, 2010). For example, in banded mongoose groups (*Mungos mungo*), male-biased survival in low rainfall conditions leads to older males participating more in helping behaviour (Marshall et al., 2016). Environmental effects of cooperation are also the subject of modelling studies, suggesting that an individual's resource acquisition ability and the levels of food availability/resource supply should determine one's contribution to cooperative foraging (Dubois and Giraldeau 2003, Liu et al. 2020). Specifically individuals that are more capable of acquiring resources should be more likely generally to invest more in cooperative behaviours, but under harsher environmental conditions (i.e. reduced resources), the relative investment of subordinate individuals in cooperative behaviours increases (as was empirically demonstrated in burying beetles, *Nicrophorus nepalensis*, Liu et al. 2020).

Intrinsic state factors are also linked to variation in the expression of conspecific cooperation (i.e. *trait frequency effects* driven by phenotypic plasticity). This includes 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 and Cant 2006). Group size may also be particularly important; for example, studies in non-human primates suggest that smaller sub-groups may be more likely to form as the total size of interacting conspecifics increases (Sih et al. 2009). Individuals then behave cooperatively with sub-group members, but there is a net increase in proportion of competitive interactions across the larger network.

Although the majority of *trait frequency effects* found here were due to phenotypic plasticity in traits, natural selection may also change the proportion of cooperative-competitive traits within a population. For example, pine engraver (*Ips pini*) phenotypes differ in their host searching behaviour (i.e. pioneers versus responders, Aukema and Raffa 2004). Exploitative responding phenotypes appear more susceptible to predation, such that elevated predation pressure may increase the proportion of cooperative pioneer phenotypes within populations.

The importance of partner identity

The identity of one's interaction partner can determine the direct and indirect fitness benefits for an individual, and their expression of cooperative-competitive behaviour. Therefore, the identities of potential interaction partners can be a factor driving *trait frequency effects* (see Fig. 1A), but may also be a key component behind *systematic variance effects* (see Fig. 1B). Particularly important for intraspecific interactions is the level of relatedness with a partner, and the potential inclusive-fitness effects. For example, in the cnidarian *Hydractinia symbiolongicarpus*, where colony fusion is determined genetically: colonies sharing allorecognition alleles fuse, whereas colonies that do not will engage in conflict (Nicotra et al. 2009). Similarly, affiliative interactions in social yellow-bellied marmot groups (*Marmota flaviventer*), appear to be structured around kin relationships between individuals, their age, and their individual social state (Wey and Blumstein 2010; Wey et al. 2019).

On the one hand, the degree of relatedness between individuals can be seen as a biotic environmental factor that may cause one to behave more or less cooperatively, for example through kin selection (Hamilton 1964), as evidenced by empirical studies highlighting the importance of partner identity in cooperative decision-making (e.g. Nicotra et al. 2009, Wey et al. 2019). On the other hand, relatedness among individuals in a group or population is also related to the level of phenotypic variation or similarity within the group, as more related individuals tend to exhibit more similar traits. Modelling results have further highlighted that higher in-group relatedness can increase the willingness of group members to contribute to offspring-rearing in collective breeding groups (Savage et al. 2013), or the likelihood with which individuals induce herd defences (Frank 1998). So here cooperation increases with increasing genetic similarity between individuals, due to inclusive fitness effects.

Cooperation between phenotypically similar, but not neccessarily related, individuals may also result from social discrimination or tag-based cooperation, where individuals may cooperate based on sharing the same (potentially arbitrary) trait. Hochberg et al. (2003) provide a model showing that when social discrimination evolves, it may cause phenotypically similar individuals to form into different, spatially distinct groups. Similarly, interaction outcomes may 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 the cases described so far, individuals preferentially cooperate with related or otherwise similar individuals, but theoretical studies suggest that the opposite -- cooperation with dissimilar individuals -- may also be beneficial. For pairs or groups of interacting individuals, variation among the interacting participants can provide direct benefits, giving rise to cooperative/mutualistic outcomes. Such benefits have been termed “social heterosis” (Nonacs and Kapheim 2007), and can be considered *systemic variance effects*. For example, Uitdehaag (2011) models a system where individuals differ in how their resource acquisition is affected by environmental fluctuations. This proposes that fitness can be buffered if individuals engage in a mutualism with partners that are different from them, so they perform well in different conditions and can support each other at different times. Such mutualisms would only emerge when there is sufficient intraspecific variation in environmental responses.

Beneficial effects of variation between participants and individual specialisation may occur in various types of interactions. For example, Barta (2016) discusses how increased role/task specialization can promote the evolution of cooperation, including where individuals use different foraging strategies or where sexes provide differing forms of parental care. Modelling of inter- or intraspecific microbial interactions suggests that the degree of functional specialisation may be non-linearly related to the qualitative outcome of interactions (Estrela et al. 2016), where intermediate levels of functional benefits provided between partners are most likely to lead to cooperative outcomes. Considering leadership hierarchies in social groups as a form of task/role specialisation, social hierarchies may make social groups more efficient but this must be counterbalanced by within-group conflict over leadership (Hamilton 2013, Pinter-Wollman et al. 2016). These studies highlight that the formation of a cooperative or antagonistic interaction relies on balancing the benefits of cooperation with the interests of the individuals, where one's interaction partner and the potential benefits it may provide are key factors. In each of the cases above, where the outcome of an interaction is based on trait similarity (or dissimilarity) between partners, there is the potential for *systemic variance effects* to emerge, as changes in the level of ITV in a population will alter the degree of differences between potential interaction partners.

Systemic variance effects

System variance effects describe cases when a change in a population's level of ITV leads to outcome variation at the population level, even if there is no trait-outcome covariation. Notably, studies in our collection focusing on such variance effects were predominantly theoretical and focused on intraspecific social interactions. For example, theory suggests that the level of ITV in fecundity can alter patterns of relatedness within neighbourhoods, which can in turn produce outcome variation at the group level (Rodrigues and Gardner 2013).

Prime examples of *systemic variance effects* concern ITV in competitive ability. For example, cooperative food sharing can emerge with greater variation in resource acquisition between individuals (Uitdehaag 2011, Barta 2016). Contrastingly, in hierarchical populations, greater ITV in competitive foraging ability may reduce cooperative foraging as it becomes detrimental to lower ranked individuals (Ranta et al. 1993). This is reflected in three-spined sticklebacks who prefer schooling with similar-sized individuals (e.g. Ranta et al. 1992). These findings suggest that phenotypic similarity in competitive ability can also promote cooperative outcomes within social groups, despite the common assumption that there is more competition between phenotypically similar individuals (see Barker et al. 2017). The direction of the effect may also be context-dependent, for example in a producer-scrounger game, when resources are scarce, individuals become less likely to exploit food patches found by others as the variation in competitive ability increases, because only the most competitive individuals have a chance to scrounge the few encountered food patches (Lee et al. 2016). But if resources are plenty, scrounging frequency goes up with increasing ITV in competitive ability because more individuals have the chance to take advantage of the large number of encountered food patches.

In competition for mating partners, if there is ITV in strength, costly displays can evolve that help resolve potential fights and thus reduce antagonistic interactions (McNamara and Leimar 2010). Again, this effect can also go in the other direction. Franz et al. (2011) find that in a model with non-heritable variation in fighting ability, increasing ability of interacting individuals to accurately assess who is strongest destabilizes cooperative turn-taking strategies. Thus, the interaction should become more antagonistic with increasing ITV in fighting ability. Furthermore, genetic variation in traits related to competitive ability such as body size can lead to indirect genetic effects, e.g. when larger individuals behave aggressively towards smaller individuals, which further increases the differences in body size. These indirect genetic effects may lead to coevolution of variation in traits such as body growth rate with the level of competitiveness-cooperativeness (Marjanovic et al. 2018), such that ITV may be directly related to interaction quality. There is substantial evidence that the level of ITV in competitive ability can lead to outcome variation in intraspecific interactions, while the direction of the effects may be positive or negative and potentially context-dependent.

Similar to variation in competitive ability, the level of ITV in mate quality or attractiveness in a population may also drive outcome variation in female-male interactions. The more variation in male quality, the more repeatable is male mate finding success, and the less willing males may be to invest in raising individual broods (Lehtonen and Kokko 2012).

Partner control mechanisms and stabilisation of cooperation via systemic variance effects

In this subsection we look at a specific *systemic variance effect* receiving particular attention: the effect of ITV in cooperative-antagonistic behaviours on the emergence, maintenance and breakdown of predominantly cooperative/mutualistic interactions. In mutualisms, individuals may cheat and employ strategies that are detrimental to their interaction partner (e.g, feeding on host tissue in cleaner-client fish mutualisms, Bshary and Grutter 2002), where ‘cheater’ phenotypes may receive a fitness advantage by gaining benefits from the partner species without reciprocating (Sachs 2013, Frederickson 2013). While this may potentially lead to mutualism breakdown (see for example a rapid shift toward parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*; Sachs and Wilcox 2006), cases of evolutionary breakdowns appear relatively rare (Sachs and Simms 2006). Furthermore, control mechanisms against antagonistic individuals are often observed, for example through partner choice (e.g. Bashary and Shaffer 2002, Jones et al. 2012) or selective provisioning of benefits based on the partner behaviour (e.g. Edwards et al. 2006). Therefore the introduction of cheater phenotypes (e.g through increasing ITV in behaviour) are often subject to trait specific selective pressures intrinsic to their mutualistic partner (i.e. sanctions) that promote and maintain high levels of mutualistic phenotypes.

Cheating also occurs in predominantly cooperative intraspecific interactions. The emergence of cheater phenotypes represents shifts towards antagonism within populations, but often occurs only at low frequencies because of negative frequency-dependent selection (Kraemer and Velicer 2014), or other costs associated with the cheating (Aukema and Raffa 2004). Control mechanisms may arise such as partner choice (Roberts 1998), or policing (i.e aggressive behaviour towards conspecifics as a punishment for mediating fitness losses due to competition, Singh and Boomsma 2015). In social insects for example, the more efficient policing is, the more cooperation (i.e. less selfish egg-laying by workers) is observed (Wenseleers and Ratnieks 2006). Models further suggest that cooperative behaviour can also be preserved through self-restraint in highly related populations, without the need for policing (Frank 1996). The partner control mechanisms of a species or the composition of policing phenotypes within a population are factors that can buffer against the introduction of more antagonistic individuals into a cooperative society and increase the overall level of cooperation.

ITV may be essential to the evolution of partner control mechanisms and the stability of primarily mutualistic/cooperative interactions even in the face of cheaters. Variation in partner quality introduced through various mechanisms (e.g. mutation, McNamara et al. 2004; individual errors in decision making; Ito et al. 2017; migration, Foster and Kokko 2006) can ensure that there are always sufficiently many cheater/defector phenotypes to incentivise the evolution and maintenance of partner control mechanisms in cooperative social groups

(McNamara and Leimar 2010) and interspecific mutualisms (Johnstone and Bshary 2008, Song and Feldman 2013). For example, Foster and 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. Analogous to cheater phenotypes, the emergence of antagonistic defector cells (e.g. through mutation) and control mechanisms appear to stabilise higher-level units of organisation in transitions to multicellularity (Michod and Roze 2001, Michod and Nedelcu 2003, see also Rainey and Kerr 2010). These may be considered as *systemic variance effects*, where an increase in ITV supplies more cheater/defector individuals, but ultimately shifts the net interaction outcome towards greater cooperation.

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 et al. 2015). In this review, we identified two mechanisms through which ITV influences outcome variation along cooperative-antagonistic continua. First, where there is trait-outcome covariance (e.g. Sinervo et al. 2007, Cantor et al. 2018), selective pressures acting on among-individual trait variation -- or phenotypic plasticity in that trait (within-individual trait variation) -- may alter the quality of the average interaction across a population (termed *trait frequency effects* here, as in Fig. 1A.). Trait-specific selection leading to outcome variation may occur due to extrinsic or intrinsic state factors (Aukema and Raffa 2004, Jones et al. 2012), and may also apply to behavioural traits (Smith and Blumstein 2008, Trillmich et al. 2018), which appear especially important in inter- and intraspecific interactions (e.g. Sinervo et al. 2007, Cantor et al. 2018). Also, geographic variation in traits (e.g. Helms and Helms Cahan 2012) suggests that demographic changes through migration are a potential source of outcome variation. State-specific expression of cooperation/antagonism-linked traits also appears common in inter and intra-specific interactions (Walker et al. 2007, Menzel and Blüthgen 2010, van Dijk et al. 2010, 2012, Marshall et al. 2016). It has long been recognised that interaction outcomes may be conditional or context-dependent, i.e. where the ecological context of an interaction, such as physical conditions or the presence of third party species alter the costs and benefits for interaction partners (Chamberlain et al. 2014; Bronstein 1994; see for example Hajek et al. 2019). While this may occur also in the absence of behavioural plasticity, we found context-dependent outcome variance associated with phenotypic plasticity to be particularly common in our collection.

Second, we described *systemic variance effects* (as in Fig. 1B), where the level of ITV in a trait in a population (as opposed to the mean value) is the factor that influences the cooperative-antagonistic outcome. As in social discrimination and kin selection contexts (Hamilton 1964, Hochberg et al. 2003), greater among-individual variation may be expected to decrease cooperation with conspecifics due to reduced indirect fitness benefits. In these cases, the outcome variance appears to manifest through state-dependent expression of cooperative-competitive behaviour at the individual level (e.g. as in Rodrigues and Gardner 2013, where the average individual would behave less cooperatively in a high ITV population). Therefore a *systematic variance effect* derived from variance in one trait may occur by inducing plasticity or selection in another trait (i.e. induce a *trait frequency effect*). While these effects are closely entwined, it is important to distinguish between mean trait and variance effects, as different individual-level processes can drive changes in the mean versus variance of traits within populations.

While processes like selection and phenotypic plasticity can shift the mean trait value within a population, the level of ITV in a population is also not constant and may be influenced by multiple processes. For example, mutation and migration/invasion may be sources of ITV and introduce rare antagonistic phenotypes in predominantly mutualistic partner species (as suggested in Foster and 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 and Weissing 2010). Additionally, phenotypic plasticity may also be a source of ITV where there is environmental variation at an individual level, and/or where individuals vary in their response to the environment (e.g. reaction norms, Nussey et al. 2007, Dingemanse et al. 2010), such as trait canalization under optimal condition (Careau et al. 2014), or exposure of cryptic genetic variation under extreme conditions (Paaby and Rockman 2014). Environmental effects can alter levels of both between- and within-individual variation, through bet-hedging strategies or sub-optimal performance (Wolf and 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 of interaction outcomes.

The level of ITV and type of trait involved are also likely to influence the nature of cooperative-antagonistic shifts and the time scale on which they happen. Both *systemic variance effects* and *trait frequency effects* can occur on the time scale of an individual life span if the traits involved show state-dependent phenotypic plasticity, or on a longer evolutionary time scale spanning multiple generations if ITV is linked to heritable genetic variation. For example, plasticity in behavioural phenotypes may occur rapidly (as in Perez-Barberia et al. 2015), but behavioural traits can also be highly consistent over time and heritable (Bergmüller et al. 2010) [e.g. dolphin foraging behaviours (per Cantor et al. 2018), which may be maternally transmitted to offspring

(Whitehead 2017)]. Moreso, expressing phenotypic plasticity and maintaining the capacity to do so (e.g. via cognitive capacities) may involve costs, which impose limits on plastic responses (Dewitt and 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 associated with an allele (e.g. Nicotra et al. 2009), changes in allele frequency in the population will have intergenerational effects in interaction outcomes. In extreme cases, selection on heritable traits can lead to qualitative evolutionary consequences, e.g.mutualistic breakdown, although this appears rare potentially due to the influence of partner control mechanisms (Frederickson 2013, 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, some themes were prominent in both empirical and theoretical studies, for example the degree of relatedness between participants. Additionally, theory suggests that ITV in mutualist quality is required to maintain host-symbiont mutualisms, because this maintains selection pressures for partner choice (e.g. Song and Feldman 2013), where partner choice in response to mutualist variation is supported by empirical evidence (Bshary and Schäffer 2002). On the other hand, studies considering the role of ITV and partner controls in maintaining stable cooperative parent-offspring and female-male interactions were largely absent. It is also notable that although many of theoretical papers in our collection remain abstract, some of the theoretical papers are 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).

There were also clear differences in topics covered in empirical and theoretical publications in our collection. Among empirical studies, we found comparable numbers of papers for intraspecific vs. interspecific interactions, but the vast majority of the theoretical papers in our data set concern intraspecific interactions (see comparative proportions of interaction scales by study type in Appendix S3, Fig. S3). 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 theoretical papers but only few 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 (e.g. Hochberg et al. 2003, McNamara and Leimar 2010). Some of the theoretical papers also concern direct benefits of variation among interacting individuals (e.g. Nonacs and Kapheim 2007, Uitdehaag 2011), a mechanism that did not appear among empirical studies. Many empirical papers, on the other hand, focus on ITV's role in determining whether the outcome of an interaction, for example between an individual plant and it's associated animal species, is antagonistic or cooperative. Such trait shifts at the individual level may then lead to *trait frequency effects*.

Are the differences in literature coverage biologically meaningful, do they represent differences in the amount of attention given to certain phenomena, or are they potentially a result of our search/screening pipeline (e.g. due to the choice of search terms, inclusion criteria etc.)? We speculate that practical considerations are a major factor, e.g. the shortage of empirical papers reporting *systemic variance effects* may exist because of the additional burden of conducting experiments where treatments manipulate population ITV, requiring replication at the population level. Similarly, experimentally testing the effect of partner control mechanisms in maintaining the evolutionary stability of mutualisms likely requires relatively longer-term, multi-generation studies, while modelling approaches are well suited to dealing with evolutionary timescales. Differences between empirical research and theory lead to some interesting suggestions for future research. Although logistically challenging, future experiments that manipulate the level of ITV 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 and Gardner 2013), or further explore the directional conditionality of *systemic variance effects* due to ITV in competitive ability (picking up from Ranta et al. 1992, 1993). 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.

We believe there is value in considering shifts on cooperation-antagonism continua from an individual perspective, as phenotypic variation among individuals is a key component of mechanisms that lead to shifts in the qualitative outcomes of interactions in ecological timeframes. There is a diverse range of traits involved (although behavioural ITV appears particularly important), wherein the level of ITV and the particular trait involved (particularly its plasticity and heritability) are likely to influence interaction-outcome variance over ecological time frames, and their long-term evolutionary implications. Notably, the research interest in this topic is greatly increasing across interaction scales and interaction types, and there is wide scope for future integration given the particularly broad scope of this topic (for further information see publication trend analysis and conceptual mapping, Appendix S3, Fig S4-S5). We also believe that applying current evidence synthesis techniques as we have here (i.e. systematic literature searches, transparently reported and reproducible review methods etc.) can promote greater integration of empirical research and theory into this topic to better inform future research.

GLOSSARY

Trait: Any characteristic of an individual organism that may or may not be be heritable, including genotype, sex, morphology, behaviour, condition, social status etc..

Intraspecific trait variation 'ITV': Variation in traits between individuals of the same species, (i.e. among-individual variation), including variation driven by phenotypic plasticity (i.e. within-individual variation; per Dingemanse et al. 2010).

Phenotypic plasticity: Phenotypic expression influenced by intrinsic or extrinsic environmental factors, including an individual's current environment (i.e. state-dependent plasticity, per Wolf and Weissing 2010), or their past/early-life environment (e.g. developmental plasticity; Dewitt and Scheiner 2004).

Scale of an interaction: The hierarchical level under consideration, e.g. cells within an individual, individuals within a population, or multiple interacting species.

State: Any element of an individual's extrinsic or intrinsic environment that is strategically relevant to their future fitness (Wolf and Weissing 2010).

Interaction quality: The outcome of an interaction along a cooperative-antagonistic continuum.

Outcome variance: Variation in interaction quality, e.g. where interaction quality differs between individuals of the same population, or the interaction quality for an individual or a population changes over time or context.

Trait frequency effect: Changes in the frequency of a trait in a population leading to a net change in interaction quality. This may apply to interactions within the population, or interactions of that population with another species or conspecific group.

Systemic variance effect: Changes in the level of ITV within a population leading to a net change in interaction quality, e.g. an interaction becomes more or less cooperative/antagonistic due to an increase or decrease in trait variation within a population.

DECLARATIONS

Acknowledgments: Thank you Niki Teunissen for assisting with database searches.

Funding: This project has received funding from the European Union’s Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 836937 (NPM). The Centre for Ocean Life is a VKR center of excellence supported by the Villum foundation. This research was funded by the German Research Foundation (DFG) as part of the SFB TRR 212 (NC³; project numbers – 316099922, 396777092, 396777467, 396777869, 396779914, 396780003, 396780988, 396782445, 396782288, 396782608).

Author contributions: All authors contributed to Conceptualization, Investigation, Writing – original draft, Writing – review & editing. In addition, NPM contributed to Data curation, Funding acquisition, Formal analysis, Methodology, Project administration, Software, Validation, Visualization. ET contributed to Data curation, Formal analysis, Software, Validation, Visualization. BC, CF, CM, JK contributed to Funding acquisition. MJW contributed to Methodology, Project administration, Supervision, Funding acquisition. Note, other than NPM and MJW, the author list is in alphabetical order.

Data accessibility: Data and code used to process our systematic searches, screening records, and the information extracted from studies that was used to produce all tables and figures presented here are all available through Open Science Framework; https://osf.io/9kfpc/ (doi: 10.17605/OSF.IO/9KFPC).

REFERENCES

Allen, W. J. et al. 2018. Intraspecific variation in indirect plant-soil feedbacks influences a wetland plant invasion. - Ecology 99: 1430–1440.

Arnqvist, G. and Rowe, L. 2005. Sexual Conflict. - Princeton University Press.

Aukema, B. H. and Raffa, K. F. 2004. Gender- and sequence-dependent predation within group colonizers of defended plants: a constraint on cheating among bark beetles? - Oecologia 138: 253–8.

Barber, I. et al. 2017. Parasitism, personality and cognition in fish. - Behavioural Processes 141: 205–219.

Barker, J. L. et al. 2017. Synthesizing perspectives on the evolution of cooperation within and between species. - Evolution 71: 814–825.

Barta, Z. 2016. Individual variation behind the evolution of cooperation. - Philosophical Transactions of the Royal Society B: Biological Sciences 371: 20150087.

Bell, M. B. 2008. Strategic adjustment of begging effort by banded mongoose pups. - Proceedings of the Royal Society B: Biological Sciences 275: 1313–9.

Bergmüller, R. et al. 2010. Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2751–2764.

Bolnick, D. I. et al. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. - The American Naturalist 161: 1–28.

Bolnick, D. I. et al. 2011. Why intraspecific trait variation matters in community ecology. - Trends in Ecology & Evolution 26: 183–192.

Bro-Jørgensen, J. 2010. Intra- and Intersexual Conflicts and Cooperation in the Evolution of Mating Strategies: Lessons Learnt From Ungulates. - Evolutionary Biology 38: 28–41.

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. - Trends in Ecology & Evolution 9: 214–217.

Brown, B. L. et al. 2012. The fine line between mutualism and parasitism: complex effects in a cleaning symbiosis demonstrated by multiple field experiments. - Oecologia 170: 199–207.

Bshary, R. and Grutter, A. S. 2002. Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. - Ecology Letters 5: 130–136.

Bshary, R. and Schäffer, D. 2002. Choosy reef fish select cleaner fish that provide high-quality service. - Animal Behaviour 63: 557–564.

Canestrari, D. et al. 2014. From Parasitism to Mutualism: Unexpected Interactions Between a Cuckoo and Its Host. - Science 343: 1350–1352.

Cantor, M. et al. 2018. Spatial consequences for dolphins specialized in foraging with fishermen. - Animal Behaviour 139: 19–27.

Careau, V. et al. 2014. Early-Developmental Stress, Repeatability, and Canalization in a Suite of Physiological and Behavioral Traits in Female Zebra Finches. - Integr Comp Biol 54: 539–554.

Cariveau, D. et al. 2004. Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. - Oikos 104: 15–26.

Chamberlain, S. A. et al. 2014. How context dependent are species interactions? - Ecology Letters 17: 881–890.

Cords, M. and Thurnheer, S. 1993. Reconciling with Valuable Partners by Long-tailed Macaques. - Ethology 93: 315–325.

Dall, S. R. X. et al. 2012. An evolutionary ecology of individual differences. - Ecology Letters 15: 1189–1198.

De Gasperin, O. and Kilner, R. M. 2015. Friend or foe: inter-specific interactions and conflicts of interest within the family. - Ecological Entomology 40: 787–795.

Dedeine, F. et al. 2005. *Wolbachia* requirement for oogenesis: occurrence within the genus *Asobara* (Hymenoptera, Braconidae) and evidence for intraspecific variation in *A. tabida*. - Heredity 95: 394–400.

Dewitt, T. and Scheiner, S. 2004. Phenotypic plasticity: Functional and conceptual approaches.

Dingemanse, N. J. et al. 2010. Behavioural reaction norms: animal personality meets individual plasticity. - Trends in Ecology & Evolution 25: 81–89.

Dubois, F. and Giraldeau, L. A. 2003. The forager’s dilemma: food sharing and food defense as risk-sensitive foraging options. - The American Naturalist 162: 768–79.

Edwards, D. P. et al. 2006. Selection for protection in an ant–plant mutualism: host sanctions, host modularity, and the principal–agent game. - Proc Biol Sci 273: 595–602.

Estrela, S. et al. 2016. Private benefits and metabolic conflicts shape the emergence of microbial interdependencies. - Environmental Microbiology 18: 1415–27.

Field, J. and Cant, M. A. 2006. Helping effort in primitively eusocial wasps. - Annales Zoologici Fennici 43: 481–487.

Foster, K. R. and Kokko, H. 2006. Cheating can stabilize cooperation in mutualisms. - Proceedings of the Royal Society B: Biological Sciences 273: 2233–2239.

Frank, S. A. 1996. Policing and group cohesion when resources vary. - Animal Behaviour 52: 1163–1169.

Frank, S. A. 1998. Inducible defence and the social evolution of herd immunity. - Proceedings of the Royal Society B: Biological Sciences 265: 1911–3.

Franz, M. et al. 2011. The evolution of cooperative turn-taking in animal conflict. - BMC Evolutionary Biology 11: 323.

Frederickson, M. E. 2013. Rethinking mutualism stability: cheaters and the evolution of sanctions. - The Quarterly Review of Biology 88: 269–95.

Ge, J. et al. 2019. Sexual cooperation relies on food controlled by females in agromyzid flies. - Animal Behaviour 149: 55–63.

Hajek, A. E. et al. 2019. Context-dependent interactions of insects and defensive symbionts: insights from a novel system in siricid woodwasps. - Current Opinion in Insect Science 33: 77–83.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. - Journal of Theoretical Biology 7: 1–16.

Hamilton, I. M. 2013. The effects of behavioral plasticity and leadership on the predictions of optimal skew models. - Behavioral Ecology 24: 444–456.

Hamilton, I. M. and Ligocki, I. Y. 2012. The extended personality: indirect effects of behavioural syndromes on the behaviour of others in a group-living cichlid. - Animal Behaviour 84: 659–664.

Hart, S. P. et al. 2016. How variation between individuals affects species coexistence. - Ecology Letters 19: 825–838.

Helms, K. R. and Helms Cahan, S. 2012. Large-scale regional variation in cooperation and conflict among queens of the desert ant *Messor pergandei*. - Animal Behaviour 84: 499–507.

Helms Cahan, S. 2001. Cooperation and conflict in ant foundress associations: insights from geographical variation. - Animal Behaviour 61: 819–825.

Hochberg, M. E. et al. 2003. Socially Mediated Speciation. - Evolution 57: 154–158, 5.

Holland, J. N. et al. 2005. Mutualisms as consumer-resource interactions. - In: Ecology of predator–prey interactions. Oxford University Press New York, pp. 17–33.

Ihara, Y. 2011. Evolution of culture-dependent discriminate sociality: a gene-culture coevolutionary model. - Philosophical Transactions of the Royal Society B: Biological Sciences 366: 889–900.

Ito, K. et al. 2017. The evolution of cooperation by negotiation in a noisy world. - Journal of Evolutionary Biology 30: 603–615.

Jensen, J. L. W. V. 1906. Sur les fonctions convexes et les inégalités entre les valeurs moyennes. - Acta Math. 30: 175–193.

Johnstone, R. A. and Bshary, R. 2008. Mutualism, market effects and partner control. - Journal of Evolutionary Biology 21: 879–888.

Jones, E. I. et al. 2012. The fundamental role of competition in the ecology and evolution of mutualisms. - Annals of the New York Academy of Sciences 1256: 66–88.

Karst, J. et al. 2008. The Mutualism–Parasitism Continuum in Ectomycorrhizas: A Quantitative Assessment Using Meta-Analysis. - Ecology 89: 1032–1042.

Komdeur, J. 2006. Variation in Individual Investment Strategies among Social Animals. - Ethology 112: 729–747.

Kraemer, S. A. and Velicer, G. J. 2014. Social complementation and growth advantages promote socially defective bacterial isolates. - Proceedings of the Royal Society B: Biological Sciences 281: 20140036.

Lee, A. E. et al. 2016. Information use and resource competition: an integrative framework. - Proceedings of the Royal Society B: Biological Sciences 283: 20152550.

Lehtonen, J. and Kokko, H. 2012. Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. - Philosophical Transactions of the Royal Society B: Biological Sciences 367: 211–221.

Liu, M. et al. 2020. Social rank modulates how environmental quality influences cooperation and conflict within animal societies. - Proceedings of the Royal Society B: Biological Sciences 287: 20201720.

Lynch, M. and Walsh, B. 1998. Genetics and analysis of quantitative traits. - Sinauer Sunderland, MA.

Marjanovic, J. et al. 2018. Modelling the co-evolution of indirect genetic effects and inherited variability. - Heredity 121: 631–647.

Marshall, H. H. et al. 2016. Variable ecological conditions promote male helping by changing banded mongoose group composition. - Behavioral Ecology 27: 978–987.

McAuliffe, K. et al. 2015. When cooperation begets cooperation: the role of key individuals in galvanizing support. - Philosophical Transactions of the Royal Society B: Biological Sciences 370: 20150012.

McNamara, J. M. and Leimar, O. 2010. Variation and the response to variation as a basis for successful cooperation. - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2627–33.

McNamara, J. M. et al. 2004. Variation in behaviour promotes cooperation in the Prisoner’s Dilemma game. - Nature 428: 745–748.

Menzel, F. and Blüthgen, N. 2010. Parabiotic associations between tropical ants: equal partnership or parasitic exploitation? - Journal of Animal Ecology 79: 71–81.

Michod, R. E. 1997. Cooperation and Conflict in the Evolution of Individuality. I. Multilevel Selection of the Organism. - The American Naturalist 149: 607–645.

Michod, R. E. and Roze, D. 2001. Cooperation and conflict in the evolution of multicellularity. - Heredity 86: 1–7.

Michod, R. E. and Nedelcu, A. M. 2003. On the reorganization of fitness during evolutionary transitions in individuality. - Integrative and Comparative Biology 43: 64–73.

Milles, A. et al. 2020. Intraspecific trait variation in personality-related movement behavior promotes coexistence. - Oikos in press.

Moher, D. et al. 2009. Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. - PLOS Medicine 6: e1000097.

Montesinos-Navarro, A. et al. 2017. Network structure embracing mutualism–antagonism continuums increases community robustness. - Nature Ecology & Evolution 1: 1661–1669.

Moran, N. P. et al. 2017. Weaving animal temperament into food webs: implications for biodiversity. - Oikos 126: 917–930.

Morris, W. F. et al. 2007. Direct and Interactive Effects of Enemies and Mutualists on Plant Performance: A Meta-Analysis. - Ecology 88: 1021–1029.

Mougi, A. and Kondoh, M. 2012. Diversity of Interaction Types and Ecological Community Stability. - Science 337: 349–351.

Müller, C. et al. 2020. The Power of Infochemicals in Mediating Individualized Niches. - Trends in Ecology & Evolution in press.

Nicotra, M. L. et al. 2009. A hypervariable invertebrate allodeterminant. - Current Biology 19: 583–9.

Niepoth, N. et al. 2018. Symbiont interactions with non-native hosts limit the formation of new symbioses. - BMC Evolutionary Biology 18: 27.

Nonacs, P. and Kapheim, K. M. 2007. Social heterosis and the maintenance of genetic diversity. - Journal of Evolutionary Biology 20: 2253–65.

Nussey, D. H. et al. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. - Journal of Evolutionary Biology 20: 831–844.

Paaby, A. B. and Rockman, M. V. 2014. Cryptic genetic variation: evolution’s hidden substrate. - Nature Reviews Genetics 15: 247–258.

Perez-Barberia, F. J. et al. 2015. State-Space Modelling of the Drivers of Movement Behaviour in Sympatric Species. - PLoS One 10: e0142707.

Pesendorfer, M. B. et al. 2016. Competing for seed dispersal: evidence for the role of avian seed hoarders in mediating apparent predation among oaks. - Functional Ecology 31: 622–631.

Pinter-Wollman, N. et al. 2016. The Effect of Keystone Individuals on Collective Outcomes Can Be Mediated through Interactions or Behavioral Persistence. - The American Naturalist 188: 240–52.

Platt, M. L. et al. 2016. Adaptations for social cognition in the primate brain. - Philosophical Transactions of the Royal Society B: Biological Sciences 371: 20150096.

Rainey, P. B. and Kerr, B. 2010. Cheats as first propagules: a new hypothesis for the evolution of individuality during the transition from single cells to multicellularity. - BioEssays 32: 872–80.

Ranta, E. et al. 1992. Size matters when three-spined sticklebacks go to school. - Animal Behaviour 43: 160–162.

Ranta, E. et al. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. - The American Naturalist 142: 42–58.

Rathke, E. M. et al. 2017. Age-dependent change of coalitionary strategy in male Barbary macaques. - Primate Biology 4: 1–7.

Riebli, T. et al. 2012. Behavioural type, status and social context affect behaviour and resource allocation in cooperatively breeding cichlids. - Animal Behaviour 84: 925–936.

Roberts, G. 1998. Competitive altruism: from reciprocity to the handicap principle. - Proceedings of the Royal Society B: Biological Sciences 265: 427–431.

Rodrigues, A. M. and Gardner, A. 2013. Evolution of helping and harming in heterogeneous groups. - Evolution 67: 2284–98.

Rodriguez-Rodriguez, M. C. et al. 2017. Functional consequences of plant-animal interactions along the mutualism-antagonism gradient. - Ecology 98: 1266–1276.

Sachs, J. L. 2013. Origins, Evolution, and Breakdown of Bacterial Symbiosis. - In: Levin, S. A. (ed), Encyclopedia of Biodiversity. 2nd ed.n. Academic Press., pp. 637–644.

Sachs, J. L. and Wilcox, T. P. 2006. A shift to parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*. - Proceedings of the Royal Society B: Biological Sciences 273: 425–429.

Sachs, J. L. and Simms, E. L. 2006. Pathways to mutualism breakdown. - Trends in Ecology & Evolution 21: 585–592.

Sachs, J. L. et al. 2004. The evolution of cooperation. - The Quarterly review of biology 79: 135–160.

Savage, J. L. et al. 2013. Intra-group relatedness affects parental and helper investment rules in offspring care. - Behavioral Ecology and Sociobiology 67: 1855–1865.

Schoepf, I. and Schradin, C. 2013. Endocrinology of sociality: comparisons between sociable and solitary individuals within the same population of African striped mice. - Hormones and Behavior 64: 89–94.

Schradin, C. et al. 2009. Testosterone Levels in Dominant Sociable Males Are Lower than in Solitary Roamers: Physiological Differences between Three Male Reproductive Tactics in a Sociably Flexible Mammal. - The American Naturalist 173: 376–388.

Schuppe, E. R. et al. 2016. The social context of a territorial dispute differentially influences the way individuals in breeding pairs coordinate their aggressive tactics. - Behavioral Ecology and Sociobiology 70: 673–682.

Sih, A. et al. 2009. Social network theory: new insights and issues for behavioral ecologists. - Behavioral Ecology and Sociobiology 63: 975–988.

Sinervo, B. et al. 2007. Models of density-dependent genic selection and a new rock-paper-scissors social system. - The American Naturalist 170: 663–80.

Singh, M. and Boomsma, J. J. 2015. Policing and punishment across the domains of social evolution. - Oikos 124: 971–982.

Smith, B. R. and Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. - Behavioral Ecology 19: 448–455.

Smith, M. F. et al. 2019. Capuchin monkeys (*Sapajus [Cebus] apella*) play Nash equilibria in dynamic games, but their decisions are likely not influenced by oxytocin. - American Journal of Primatology 81: e22973.

Song, Z. and Feldman, M. W. 2013. Plant-animal mutualism in biological markets: evolutionary and ecological dynamics driven by non-heritable phenotypic variance. - Theoretical Population Biology 88: 20–30.

Speed, M. P. and Franks, D. W. 2014. Antagonistic evolution in an aposematic predator-prey signaling system. - Evolution 68: 2996–3007.

Stopka, P. and Johnson, D. D. P. 2012. Host-parasite dynamics lead to mixed cooperative games. - Folia Zoologica 61: 233–238.

Surbeck, M. et al. 2017. Male reproductive skew is higher in bonobos than chimpanzees. - Current Biology 27: R640–R641.

Székely, T. et al. 2006. Sexual Conflict, Ecology, and Breeding Systems in Shorebirds. - BioScience 56: 801.

Székely, T. et al. 2007. Sexual conflict over parental care: a case study of shorebirds. - J Ornithol 148: 211–217.

Takahashi, L. S. et al. 2017. Turn-taking ceremonies in a colonial seabird: Does behavioral variation signal individual condition? - The Auk 134: 530–541.

Thomas, M. J. et al. 2016. Ontogenetic shifts in a freshwater cleaning symbiosis: consequences for hosts and their symbionts. - Ecology 97: 1507–17.

Thompson, J. N. 1988. Variation in Interspecific Interactions. - Annual Review of Ecology and Systematics 19: 65–87.

Tilman, D. et al. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? - Am Nat 151: 277–282.

Trillmich, F. 2010. Parental care: adjustments to conflict and cooperation. - In: Kappeler, P. (ed), Animal Behaviour: Evolution and Mechanisms. Springer Berlin Heidelberg, pp. 267–298.

Trillmich, F. et al. 2018. Understanding the evolution of personality requires the study of mechanisms behind the development and life history of personality traits. - Biology Letters 14: 20170740.

Uitdehaag, J. C. 2011. Bet hedging based cooperation can limit kin selection and form a basis for mutualism. - Journal of Theoretical Biology 280: 76–87.

Uriarte, M. and Menge, D. 2018. Variation between individuals fosters regional species coexistence. - Ecology Letters 21: 1496–1504.

van Dijk, R. E. et al. 2010. Sexual conflict predicts morphology and behavior in two species of penduline tits. - BMC Evolutionary Biology 10: 107.

van Dijk, R. E. et al. 2012. Individual variation and the resolution of conflict over parental care in penduline tits. - Proceedings of the Royal Society B: Biological Sciences 279: 1927–36.

Violle, C. et al. 2012. The return of the variance: intraspecific variability in community ecology. - Trends in Ecology & Evolution 27: 244–252.

Vorburger, C. et al. 2013. Comparing constitutive and induced costs of symbiont-conferred resistance to parasitoids in aphids. - Ecol Evol 3: 706–713.

Walker, F. M. et al. 2007. Does soil type drive social organization in southern hairy-nosed wombats? - Molecular Ecology 16: 199–208.

Wenseleers, T. and Ratnieks, F. L. W. 2006. Enforced altruism in insect societies. - Nature 444: 50–50.

West, S. A. et al. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. - Journal of Evolutionary Biology 20: 415–432.

Westgate, M. J. 2019. revtools: An R package to support article screening for evidence synthesis. - Research Synthesis Methods 10: 606–614.

Westneat, D. F. et al. 2015. The biology hidden inside residual within-individual phenotypic variation. - Biological Reviews 90: 729–743.

Wey, T. W. and Blumstein, D. T. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. - Animal Behaviour 79: 1343–1352.

Wey, T. W. et al. 2019. Transitivity and structural balance in marmot social networks. - Behavioral Ecology and Sociobiology in press.

Whitehead, H. 2017. Gene–culture coevolution in whales and dolphins. - PNAS 114: 7814–7821.

Whiteman, E. A. and Côté, I. M. 2004. Dominance hierarchies in group-living cleaning gobies: causes and foraging consequences. - Animal Behaviour 67: 239–247.

Wolf, M. and Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 3959–3968.

Yuan, Z. L. et al. 2011. From pattern to process: species and functional diversity in fungal endophytes of *Abies beshanzuensis*. - Fungal Biology 115: 197–213.

SUPPORTING INFORMATION

Appendix S1. Search strategy and information sources.

Appendix S2. Study selection.

Appendix S3. Publication trends and bibliometric analysis.

Appendix S4. Included studies summary information