REVIEW AND SYNTHESIS

Cheaters must prosper: reconciling theoretical and empirical perspectives on cheating in mutualism

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Abstract

Cheating is a focal concept in the study of mutualism, with the majority of researchers considering cheating to be both prevalent and highly damaging. However, current definitions of cheating do not reliably capture the evolutionary threat that has been a central motivation for the study of cheating. We describe the development of the cheating concept and distill a relative-fitness-based definition of cheating that encapsulates the evolutionary threat posed by cheating, i.e. that cheaters will spread and erode the benefits of mutualism. We then describe experiments required to conclude that cheating is occurring and to quantify fitness conflict more generally. Next, we discuss how our definition and methods can generate comparability and integration of theory and experiments, which are currently divided by their respective prioritisations of fitness consequences and traits. To evaluate the current empirical evidence for cheating, we review the literature on several of the best-studied mutualisms. We find that although there are numerous observations of low-quality partners, there is currently very little support from fitness data that any of these meet our criteria to be considered cheaters. Finally, we highlight future directions for research on conflict in mutualisms, including novel research avenues opened by a relative-fitness-based definition of cheating.

Keywords

Ant–plant, cleaner fish–client, cooperation, fig–fig wasp, fitness conflict, legume–rhizobia, nectar larceny, partner quality, plant–mycorrhizae, yucca–yucca moth.

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INTRODUCTION

Mutualisms are defined by the reciprocal net benefit that heterospecific partners receive through the exchange of resources and services. Although the outcome of mutualism is mutually beneficial, the underlying actions are self-interested – individuals are expected to maximise their own net benefits without regard to the consequences for their partners. Thus, unless the interests of partners are perfectly aligned, there should be an incentive to 'cheat' (Trivers 1971; Soberon & Martinez del Rio 1985).

However, while there is widespread agreement that cheating is a fundamental concept in the study of mutualism, there has been very little consensus on the definition of cheating itself

(Ghoul *et al*. 2014; Box 1, Fig. 1). There has been disagreement over what needs to be measured in order to determine whether cheating is happening, as well as which partner is the focus of such measurements. The literature also contains varying definitions regarding how distinct cheaters are from other partners and whether phylogenetic restrictions should be imposed on who can be considered a cheater (Table 1). These differing definitions have led to inconsistency over how cheating is identified and modelled, hampering our ability to determine how common cheating is and to predict how mutualisms will evolve.

Adoption of a fitness-based definition of cheating has great promise to promote comparability across studies and systems. Yet, the definition that has been proposed – that cheating increases individual fitness and reduces partner fitness (Ghoul

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Box 1 Current opinions about cheating

As studies of cheating in mutualism have accumulated, so have definitions of cheating (Table 1, Fig. 2). To evaluate current perspectives in the community, we conducted an anonymous survey of professional ecologists and evolutionary biologists (Supporting Information S1). Of the respondents who self-identified as working on mutualism, 30% also identified that they work on cheating. The average response to 'How common is cheating in mutualisms?' was 2.476, with answers ranging from 1 to 4 on a scale of 1 (nonexistent) to 5 (ubiquitous). The average response to 'How much of a threat does cheating pose for the persistence of mutualisms?' was 2.825, with answers ranging from 1 to 5 on a scale of 1 (no threat) to 5 (extreme threat). Individuals rated the threat of cheating to be higher than its prevalence (paired t-test, $P = 0.0351$). Respondents were asked to evaluate seven potential definitions of cheating from the literature on a scale of 1 (completely disagree) to 5 (completely agree). Of the potential definitions, only 'a cheater provides no reward' was disagreed with on average. The potential definition that received the most agreement was 'a cheater has a higher reward taken: reward given ratio than other prospective partners'. The level of agreement for each of the seven potential definitions is shown in Fig. 1.
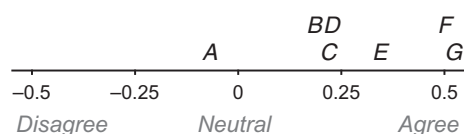
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Table 1 Variation in the concept of cheating. Major aspects of the definition of cheating and the alternate perspectives that appear in the empirical and theoretical literatures on cheating in mutualism (for a review of alternative definitions see Ghoul *et al.* 2014, table A1).

Aspect of the cheating definition	Alternate perspectives
What needs to be measured	• Mutualist rewards • Specific antagonistic behaviours • **Net fitness effects**
Who needs to be measured	• The putative cheater alone • Multiple individuals for comparison • Both the putative cheater and its partner • **Multiple partner combinations**
How different cheaters are from non-cheaters	• Discretely different • **Quantitatively different**
Phylogenetic restrictions	• None • **Only members of (previously) mutualistic lineages can be considered cheaters**

The perspectives that correspond with our definition (a cheater must have higher than average relative fitness and cause its partner to have lower than average relative fitness) are given in bold.

Figure 1 Survey responses on the definition of cheating. Respondents were asked to evaluate seven potential definitions of cheating from the literature on a scale of 1 (completely disagree) to 5 (completely agree); we re-scaled these responses to calculate the overall extent of agreement ranging from −1 to +1. Ordered from least to most agreement, the definitions were (A) a cheater provides no reward, (B) a cheater takes more reward than other potential partners, (C) a cheater takes a benefit but does not provide a reward, (D) a cheater takes more than its fair share, (E) a cheater provides less than its fair share, (F) a cheater provides less reward than other potential partners and (G) a cheater has a higher reward taken: reward given ratio than other prospective partners.

et al. 2014) – implies a comparison without specifying what needs to be compared. Here, we provide a brief history of the development of the cheating concept in the mutualism literature. We then introduce a definition of cheating based on relative fitness that builds upon previous work and describe methods for measuring cheating and fitness conflict in future studies. We discuss the advantages of our definition, particularly for the reconciliation of theoretical and empirical perspectives on cheating, and use it to re-evaluate classic empirical examples of cheating. Finally, we propose emerging research directions to move the field beyond its current focus on identifying cheaters and towards theoretical and empirical integration. Ultimately, this integration will enable us to make quantitative predictions about the benefits and ecosystem services generated by mutualisms.

A BRIEF HISTORY OF THE CHEATING CONCEPT

Individuals and species that are associated with mutualisms but do not confer benefits have been noted since biologists first began studying mutualisms. For example, in 1878 Kerner wrote an entire book entitled 'Flowers and their Unbidden Guests', a product of his years of studying pollination biology under the influence of Charles Darwin. Many early examples were summarised in 'Parasitism and Symbiosis', published by Caullery in 1952. Through at least the mid-1980s, the ecological literature used a wide diversity of terms to describe these phenomena. For instance, ants that occupied acacias without defending their hosts were termed 'parasites' (Janzen 1975), the phenomenon in which orchids lured pollinators to non-rewarding flowers was called 'deception' (Vogel 1978), and floral visitors that collected nectar without pollinating were defined as 'robbers' or 'thieves' depending on their mode of entry to the flower (Inouye 1980). By the time the first lengthy review of mutualism was written (Boucher *et al.* 1982), the ubiquity of these apparent cheating behaviours was well-recognised.

Through the 1980s, interpretations of the causes and consequences of cheating in mutualisms developed largely in the absence of any theoretical framework (but see, e.g. Brower *et al.* 1970 in the context of Mullerian mimicry). This began to change with the publication of Axelrod and Hamilton's seminal 1981 paper on the evolution of cooperation. Although previous authors had made some of the same points (e.g. Rapaport & Chammah 1965; Trivers 1971), two influential elements of Axelrod & Hamilton (1981) were (1) that the advantage of cheating poses a fundamental problem to the evolutionary persistence of cooperation and (2) that this prob-
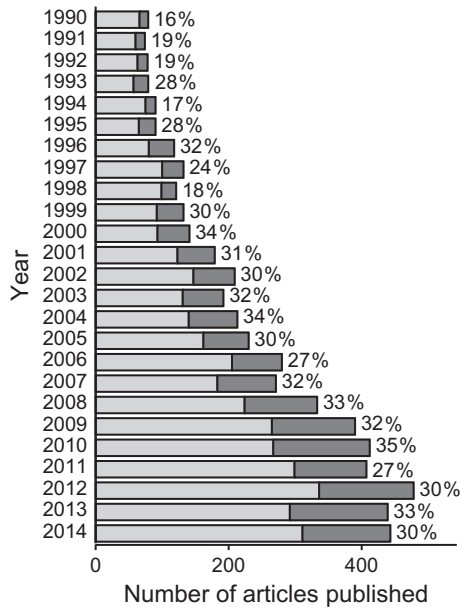
Figure 2 Prevalence of the cheating concept in studies of the evolution of mutualism. The number of articles on the evolution of mutualism per year with (dark grey) and without (light grey) a keyword relating to cheating are shown. The percentage of papers with a keyword about cheating is next to the bar. A search was conducted on Thomson Reuters Web of Science of all articles published between 1990 and 2014. The total number of articles per year on the evolution of mutualism was counted as the number with topic keywords = mutualis* AND evol*). The subset of articles per year with a keyword relating to cheating was counted as the number with topic keywords = (mutualis* AND evol*) AND (cheat* OR exploit* OR parasit* OR conflict* OR defect*).

lem is shared by both intraspecific and interspecific (i.e. mutualistic) interactions. Axelrod and Hamilton's game theory approach was rapidly adopted and applied to understanding how mutualism can persist evolutionarily. In other words, Axelrod and Hamilton's paper immediately raised cheating from a well-known and well-documented ecological feature of mutualisms to the focal evolutionary paradox of mutualisms.

Since the 1980s, the theoretical and empirical literature on cheating in mutualism has proliferated (Fig. 2); 31% of mutualism publications about the evolution of mutualism in the last 5 years also explore cheating. Mutualism theory has diverged from the within-species cooperation literature and focused on mechanisms that reduce conflict between species (Box 2). Meanwhile, new empirical examples deemed to be cheating have continued to accumulate at a rapid pace, leading to several general reviews (Bronstein 2001, 2003; Yu 2001; Douglas 2008; Frederickson 2013; Ghoul *et al.* 2014) as well as others on specific systems (Smithson 2009; Irwin *et al.* 2010; Friesen 2012).

A STANDARD FRAMEWORK FOR STUDYING CHEATING AND FITNESS CONFLICT

As the studies on cheating in mutualism have multiplied, so have the definitions of cheating. Both the literature (reviewed in Ghoul *et al.* 2014) and a survey of practicing ecologists and

Box 2 Theoretical mechanisms that favour costly mutualistic behaviours

The main mechanisms that have been proposed to stabilise mutualism against cheating fall into two general categories. In the first category, partner fidelity, future rewards depend on current investment through positive feedbacks between the fitnesses, or fitness components, of partners (Bull & Rice 1991; Sachs *et al.* 2004). These feedbacks are produced when the same individuals or their relatives are likely to interact repeatedly due to spatial structure in the interacting populations (Frank 1994; Doebeli & Knowlton 1998) or vertical transmission between successive generations (Yamamura 1996). In the second category, partner control, an individual's phenotype has a direct effect on the response it receives from its partner (reviewed in Bshary & Bronstein 2011; Jones *et al.* 2012). At the initiation of an interaction, partner choice or screening can be used to select partners based on signals or cues of their quality (Bull & Rice 1991; Noe & Hammerstein 1994; Sachs *et al.* 2004; Archetti *et al.* 2011). Alternatively, individuals may gradually increase their investment in each other through successive rounds of negotiation if they have received acceptable offers in previous rounds (Roberts & Sherratt 1998; Akcay & Roughgarden 2007). In contrast, sanctions may be used to punish inferior partners by decreasing rewards, inflicting additional costs, or terminating the interaction (Denison 2000; West *et al.* 2002a).

evolutionary biologists (Box 1, Fig. 1) suggest a widespread lack of clarity over what cheating means. Problematically, the different definitions have fundamental disparities (Table 1) that result from the frequent confounding of *whether* cheating is happening with *how* cheating can happen. At best, the multiplicity of definitions obscures insights that could be gained from synthesizing across studies. At worst, the failure to recognise that others are using incompatible definitions can lead to misunderstandings about the prevalence and threat of cheating.

Here, we present our argument for defining cheating in terms of the relative fitness consequences of particular strategies to each partner. We complement our definition with a description of experimental methods to identify cheaters. Additionally, we suggest methods for measuring fitness conflict between mutualist species, which can give additional insight into the mutualism.

Refining the definition of cheating

We contend that a definition of cheating must do three things: be informative about the threat posed to the mutualism, explicitly prescribe how cheating can be identified and enable comparability across studies and systems. In order to pose a threat to the mutualism, cheating must both erode the benefit gained by the partner and also be evolutionarily favoured so that it can spread. These effects can only be captured by rela-

tive fitness criteria. Defining cheating in terms of relative fitness also meets the second two requirements by providing a clear, standardised unit of measurement. Cheating must therefore (1) *increase the fitness of the actor above average fitness in the population* and (2) *decrease the fitness of the partner below average fitness in the partner population* (Fig. 3). When only criterion (2) is met, low-quality mutualists are bad for their partners, but they will not spread. These individuals are defective, rather than defectors (Friesen 2012). When only criterion (1) is met, the strategy that increases actor fitness will spread, but it will not harm either the partner or the mutualism. Critically, measuring just the rewards exchanged between partners is not sufficient for identifying whether there is a threat to the mutualism, since the relationship between rewards and fitness is not straightforward. In particular, rewards may not be costly to produce (i.e. by-product mutualism; Sachs *et al.*
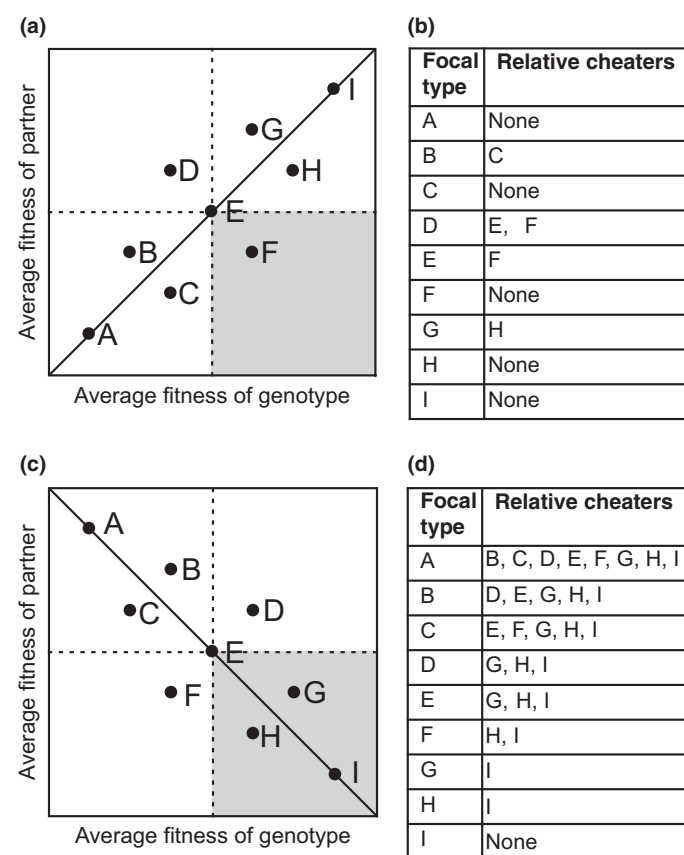
2004; Douglas 2008), fitness benefits may saturate so that additional reward does not increase fitness, and there may be feedbacks that make the reward received dependent on the reward given (Box 2; Figs 4 and 5). Although it is possible in principle to infer fitness consequences from mutualist traits, we currently lack the quantitative understanding required to conclude that cheating is occurring from phenotypic data alone.

It is instructive to compare the definition of cheating given here with the standard definitions for mutualism and parasitism. We define cheating through comparison to the average
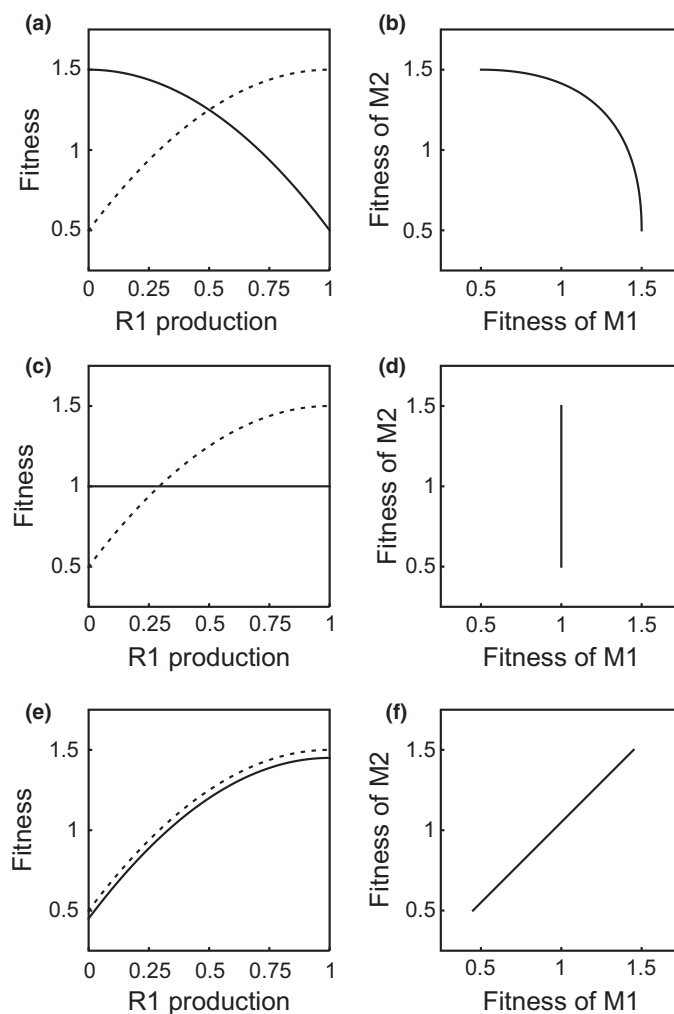

Figure 3 Identifying cheaters by pairwise and population comparisons. In a pairwise comparison, one genotype is considered to be a cheater relative to another if it has higher fitness but causes lower partner fitness. Given overall fitness alignment between genotypes A-I of species 1 and their partners in species 2 (a), pairwise comparisons of genotypes A-I lead to inconsistent identification of cheaters (b). Given overall fitness conflict (c), pairwise comparisons result in a nested identification of cheaters (d). Moreover, some genotypes identified as cheaters in pairwise comparisons would not fulfil the conditions to both increase in the population and decrease average partner fitness. Only genotypes that fall significantly into quadrant IV (grey), i.e. that have above-average fitness and cause below-average partner fitness, meet these conditions and should be considered cheaters at the population level. Therefore, the only cheaters are genotypes F as shown in (a) and G, H, and I as shown in (b).

Figure 4 Linking rewards exchanged to fitness outcomes. If reward production is costly and there are no feedbacks in reward exchange, mutualist M1's fitness (solid) decreases as it produces more reward R1; meanwhile, partner M2's fitness (dashed) increases with R1 received (a). Consequently, there is fitness conflict between M1 and M2 (b). Any reduction in R1 production constitutes cheating by M1, as it gains a fitness benefit at a fitness cost to M2 (though the cost is small if M2's fitness is saturating). However, if R1 is a by-product and not costly to produce, M1's fitness does not change with amount of R1 produced (c). Therefore, M1 cannot cheat by producing less R1, because there is no fitness advantage (d). Finally, if there is a feedback between rewards exchanged, both partners have higher fitness when more R1 is produced (e). Thus, there is fitness alignment (f) and M1 cannot cheat.
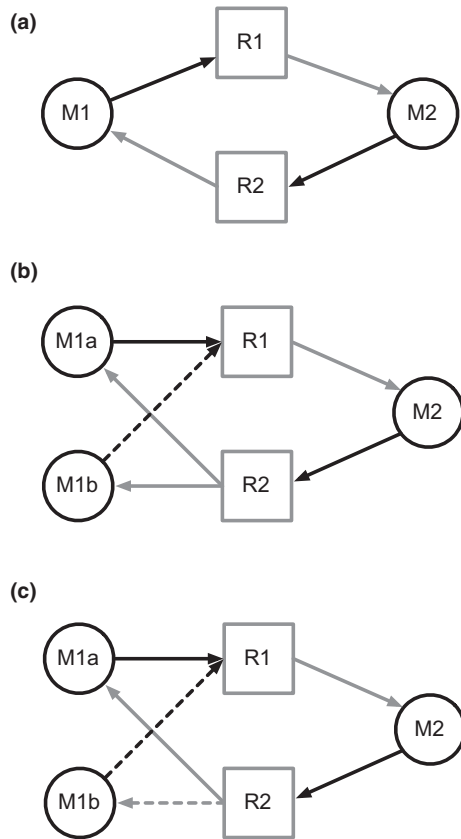
Figure 5 Reward exchange and cheating. Mutualists M1 and M2 produce rewards R1 and R2, respectively, and consume the reward produced by the partner (a). The arrows show reward production (black) and reward consumption (grey). Assuming that fitness is a monotonic function of each reward exchanged and that there are no feedbacks coupling these exchanges, the individual M1b can be a cheater relative to M1a by providing less reward to the partner, M2 (b). However, M1b should not be considered a cheater if it not only gives a small reward but also receives a comparably small reward (c). This case could result from M1b being defective and unable to take a larger reward or from mechanisms that thwart cheating by causing feedbacks between the amount of reward given and the amount of reward received. (Modified from Jones *et al.* 2012).

fitness consequences of an interaction. Meanwhile, at the individual level, mutualism and parasitism are defined through comparison to the absence of an interaction. There is mutualism when each individual has higher fitness with the interaction than without the interaction. Parasitism entails a fitness increase for one individual and a decrease for the other, compared to their fitnesses in the absence of an interaction. As a consequence of the different comparison points, a cheater may be either a mutualist or a parasite. A cheater will still be a mutualist as long as it provides a net fitness benefit to the partner. Interacting with such a cheater is worse than interacting with the average partner, but it is still better than having no partner at all. Alternatively, cheaters might reduce partner fitness compared to no interaction and thus be parasites as well.

It is also important to note that not all parasites should be considered cheaters. Implicit in the definition given here is the restriction of cheating to members of mutualistic lineages. The

evolution of cooperation in general is considered a central problem in evolutionary biology because of selection for cheating within cooperative populations. The 'temptation to defect' implies pre-existing cooperation, and therefore the emergence of cheaters from within previously cooperative populations or lineages. Therefore, in agreement with some earlier treatments of cheating (Bronstein 2001; Frederickson 2013), our definition requires that cheaters must be derived from cooperators. Species that are not derived from cooperators may be parasites; however, these species pose an external threat to the mutualism, whereas cheaters pose a threat from within.

How to identify cheaters

When using other definitions of cheating, categorizing individuals as cheaters is only straightforward when the definition specifies a particular strategy or when there are just two strategies to compare. When partners vary continuously in quality, 'a new and more subtle kind of cheating becomes possible' (Roberts & Sherratt 1998) and comparisons of pairs of individuals can lead to an inconsistent identification of cheaters (Fig. 3). For example, strains of rhizobia vary continuously in the amount of nitrogen they provide to their legume hosts and they obtain varying amounts of carbon in return (Thrall *et al.* 2000). When strategies vary continuously, some 'cheaters' identified using pairwise comparisons will pose no threat to the mutualism, as they will have below-average fitness in the population. Meanwhile, other 'cheaters' may provide an average or even above-average fitness benefit to their partners (Fig. 3). We thus caution against the use of pairwise comparisons when identifying cheating.

To identify cheaters within the framework of our relative-fitness definition, the putative cheaters' fitness must be compared against the weighted population averages for fitness and partner fitness (Fig. 3; see details in Box 3). The most dangerous strategies from the perspective of mutualism stability will not necessarily be the worst partners in terms of quality; they will be those that lead to the greatest fitness conflict, i.e. those that simultaneously maximise individual fitness gain and partner fitness loss. It is also important to note that identification of cheaters using relative fitness only predicts near-term evolutionary dynamics. Whether cheaters proceed to erode the mutualism or not depends on the relative fitness of other strategies as well as on the evolution of the partner. A genotype identified as a cheater might be expected to decrease in frequency in the near future, despite currently having above-average fitness, if more beneficial strategies have even higher relative fitness (e.g. Fig. 3a). Individuals are only cheaters if they prosper, but that does not necessarily mean they will prosper for very long.

Beyond cheating: measuring fitness conflict

Cheating is fundamentally a manifestation of fitness conflict between partners (Fig. 3c). Unless cheaters are just emerging, measuring the extent of fitness conflict is likely to be more informative about the evolutionary dynamics of the mutualism than identifying particular individuals as cheaters would be. Fitness conflict can be quantified in two ways: measuring fitness correlations or conducting selection analysis for each

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Box 3 How to measure cheating and quantify fitness conflict

A cheating strategy must (1) have increased relative fitness and (2) decrease partner relative fitness compared to the population mean fitnesses. In order to determine these fitness correlations, the ideal design is a full-factorial pairing of partners with fixed genotypes, such as inbred lines, full-sib families or single microbial isolates. An experimental approach would be required to determine the distribution of potential fitness benefits among interacting partner lineages due to mutualism. Alternatively, observational measurements of fitness under natural conditions could yield informative data for species not amenable to experimentation. For long-lasting mutualist associations, the most relevant measurement would be the lifetime fitness of each partner, especially since costs to one fitness component may be balanced by benefits to another fitness component (e.g. Palmer *et al.* 2010). However, when lifetime fitness is problematic to measure and for short-term associations that may have relatively small individual contributions to lifetime fitness, fitness proxies relevant to the interaction may be more practical to measure. If the rewards exchanged between partners are measured, they will be informative about cheating only if the relationship between rewards and each partner's fitness is known. Therefore, the fitness costs and benefits of the rewards must be measured. The same calculations below can then be used with fitnesses calculated using the known phenotype–fitness relationships. Because many mutualisms are context dependent, measurements taken under different ecological conditions may lead to different relationships between partner fitnesses (Box 4). Finally, in systems where the individual is not the relevant unit of selection (e.g. social insects), fitness variation at the correct level (e.g. the colony) would need to be related to the mutualist strategies present.

Step 1: Measure the fitness of each partner alone. This provides the baseline for determining whether their interaction is mutualistic (i.e. each has higher fitness together than alone) or parasitic.

Step 2: Measure the fitness of each partner genotype M1i and M2j in factorial pairings over a random sample of i's and j's in realistic environmental conditions or over multiple environments to explicitly study the contexts under which cheating might occur (see Box 4).

Step 3A: Calculate the correlation between the fitnesses of M1 and M2. The sign and magnitude of the correlation provide an estimate of fitness conflict or alignment between the species.

Step 3B: Calculate the selection gradient for each partner to determine if there is asymmetrical selection for cheating. Treat the average fitness of M2 when M1i is the partner as a phenotype of M1i and conduct a standard selection analysis; similarly, treat the average fitness of M1 when M2j is the partner as a phenotype of M2j. Selection on M1 to decrease the fitness of M2, or vice versa, is evidence of fitness conflict. If experimentally controlled individual genotypes are available, a genetic selection analysis should be preferred. However, a phenotypic selection analysis with unknown genotypes would still yield insight into the patterns of selection. Two caveats with phenotypic selection analysis are (1) predicting the response to selection is not possible without knowledge of heritability and (2) environmental variation can lead to positive relationships between partner fitnesses since both partners may perform better in higher quality environments.

Step 4: To categorise particular genotypes as cheaters, they must be compared to the population average. A cheater must have higher relative fitness than average and cause its partner to have lower relative fitness than average. In particular, total lifetime fitness is the basis of this calculation, not just the component of fitness due to the interaction – this accounts for potential trade-offs between engaging in mutualism and other components of fitness. We note that fitness conflict may be present even if no genotypes can be categorised as cheaters, especially when fitness variation has a large random component.

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partner's effect on the other's fitness. Empirical procedures for these two approaches are outlined in Box 3, with additional consideration of context dependency discussed in Box 4. When fitness correlations are measured, a negative genetic correlation between actor and partner fitness suggests that cheating is widespread (e.g. Fig. 3c); conversely, a positive correlation is evidence for overall fitness alignment (e.g. Fig. 3a; Friesen 2012), although cheaters could still be present at low frequency. Meanwhile, in selection analyses, one partner's fitness can be treated as a trait of the other partner (e.g. Porter & Simms 2014; Box 3). In a genotypic selection analysis, the selection gradient of the focal partner is determined using the fitness of each genotype of that species averaged across potential partners. Selection on the focal species to reduce its partners' fitness is evidence of fitness conflict. This conflict can be distinct from overall fitness conflict or alignment (e.g. Heath 2010) since it is not necessarily symmetrical between the partners.

Genotypic selection analysis gives stronger evidence for fitness conflict or alignment than phenotypic selection analysis, since it eliminates the confounding effect of environmentally induced covariance between each partner's fitness. If partners interact across a heterogeneous environment, both may have low fitness in poor quality patches and high fitness in high-quality patches, resulting in a positive fitness correlation among individuals even if there is underlying fitness conflict among genotypes. A quantitative genetic approach with inbred lines is possible in systems such as annual legumes and their associated rhizobia, but is more challenging in long-lived or difficult to cultivate organisms.

RECONCILING THEORETICAL AND EMPIRICAL PERSPECTIVES ON CHEATING

In examining the theoretical and empirical perspectives on cheating in mutualism, we have identified a tension between

the empirical focus on phenotypes, or 'cheating actions', and the theoretical focus on fitness, or 'cheating outcomes'. Here, we discuss the conflict between these perspectives and how adopting a relative-fitness-based definition of cheating can help resolve the conflict.

Cheating actions vs. cheating outcomes

In many cases, there appears to be a clear connection between a less cooperative strategy and both increased individual fitness and decreased partner fitness (e.g. Figs. 4a, b, and 5b). However, the link between a potential cheating action and these fitness outcomes can be broken in two ways.

First, low-quality partners may simply be 'making the best of a bad job'. For example, if individuals vary in how many resources they have, individuals that provide less reward do not necessarily end up with a fitness advantage over individuals that provide more reward. However, low-quality partners that are not hoarding resources but simply have fewer to give to the partner are not theoretically interesting and thus not included in models (but see Sherratt & Roberts 2001). Thus, in models, there is generally no need to question whether low-quality partners are cheaters or just defective partners. In the real world, variation in partner quality can be maintained by factors other than the fitness advantages of cheating, such as mutation–selection balance, wherein low-quality mutualists recurrently evolve but are purged from populations (reviewed in Heath & Stinchcombe 2014).

Second, the outcome of the interaction depends on more than just one individual's strategy. As soon as stabilizing mechanisms such as partner fidelity feedback, partner choice or sanctions (Box 2) are implemented, cheating actions are no longer guaranteed to result in a fitness advantage (e.g. Figs 4e, f and 5c). In models, the mechanisms that maintain fitness alignment can be turned on and off, revealing the hypothesised high-fitness cheaters that are thwarted when stabilizing mechanisms are active. Turning off the empirical mechanisms that maintain cooperation to see whether actions that would be cheating are being thwarted is much more difficult, although it is sometimes possible to prevent partner choice from occurring by restricting access to alternative partners. Similarly, if there is natural variation in the degree to which one mutualist exerts control over the other, then one could test whether the fitness of low-quality partners is higher with genotypes that have weaker control. However, it is typically unknown whether uncooperative actions could have paid off if not for the stabilizing mechanism.

Since potential cheating actions do not always lead to cheating outcomes, it is critical to recognise that phenotypic and fitness perspectives of cheating are not interchangeable. Cheating must be defined on either the basis of phenotype or fitness. Only a relative-fitness definition is reliably informative about the threat to the persistence of the mutualism; we argue that it is therefore more consistent with the underlying motivation for studying cheating. Acknowledging the distinction between cheating actions and cheating outcomes will help close the gap between theoretical and empirical perspectives over the prevalence of cheating in nature.

Cheating can occur through multiple mechanisms

Early game theoretical models of mutualism focused on cheating by providing less reward to the partner (Trivers 1971; Axelrod & Hamilton 1981) and most recent theory has kept that focus (e.g. Doebeli & Knowlton 1998; Ferriere *et al.* 2002; West *et al.* 2002b; Foster & Kokko 2006; Friesen & Mathias 2010). Yet, empirical studies have revealed that there can be fitness conflict over other aspects of the mutualism, especially the extraction of benefits from the partner. As described in more detail in our review of empirical evidence below, individuals may vary in both how much reward they take and in the kinds of rewards they take. However, few models have considered cheating by extracting a greater benefit (e.g. seeds in the case of pollinating seed predators; Jones *et al.* 2009) or an additional type of benefit (e.g. host tissue in the case of cleaner fish; Poulin & Vickery 1995; Johnstone & Bshary 2008) from the partner. Variation in providing benefits and extracting benefits are not mutually exclusive and can be investigated simultaneously, but this has rarely been done (but see Ferdy *et al.* 2002).

An advantage of a fitness-based definition of cheating is that it encompasses a greater diversity of strategies that can threaten the evolutionary stability of mutualisms. By promoting recognition of these other strategies as forms of cheating, we can open the way for studies comparing types of cheating.

Cheating should be rare

Models of cheating in mutualism assume the existence of fitness conflict, i.e. the 'temptation to defect'. These models thus typically do not test whether low-quality partners meet the criteria for cheating at different points in the evolution of the mutualism, but rather simply track the distribution of partner quality (e.g. Foster & Kokko 2006). However, they then generally predict that cheating should be rare – cheating is either transient as the mutualism itself collapses (Trivers 1971; Axelrod & Hamilton 1981) or it is eliminated by the mechanisms that prevent the collapse of the mutualism.

When selection leads to a monomorphic equilibrium at which all partners provide the same net benefit (e.g. Foster & Kokko 2006; Johnstone & Bshary 2008), the point of comparison between cheaters and cooperators is lost. Although no individual is being as cooperative as it could be, no individual is gaining a fitness advantage by being a worse partner either. Even when variation in partner quality is maintained at the evolutionary equilibrium, low-quality partners often do not meet the fitness criteria to be considered cheaters. When variation is maintained at a stable equilibrium by selection alone, then by definition, all phenotypes must have equal fitness on average. For example, negative frequency-dependent selection on partner quality may lead to a polymorphic equilibrium due to nonlinear trade-offs between partner quality and competition for rewards (Law *et al.* 2001; Ferdy *et al.* 2002; Ferriere *et al.* 2002) or imperfect partner control mechanisms (Friesen & Mathias 2010). However, at the equilibrium, there are no cheaters because low-quality partners have the same fitness, on average, as high-quality partners. Low-quality partners may also be maintained in the population by mutation–selec-

tion balance or epistasis, even if they have lower fitness than higher quality partners (Foster & Kokko 2006; Heath & Stinchcombe 2014).

The persistence of low-quality partners that are cheaters according to a fitness-based definition could be explained by either spatial structure or spatial and/or temporal variation in environmental conditions. In spatial models with limited dispersal and local interactions, high-quality partners may persist by colonizing empty patches at least as fast as cheaters invade and drive high-quality partners locally extinct (e.g. Frank 1994; Doebeli & Knowlton 1998; Szilagyi *et al.* 2009). Meanwhile, fluctuations in environmental conditions can lead to variation in the costs and benefits of mutualism and thus to varying selection on partner quality and the maintenance of multiple partner quality strategies (e.g. Nuismer *et al.* 2003). In these cases, low-quality partners may be cheaters in some environments; however, if they were cheaters in all environments, they would be expected to lead to the collapse of the mutualism.

The general theoretical expectation that cheating should be rare is at odds with the many empirical descriptions of cheating. Adoption of a relative-fitness-based definition clarifies that not all variation in partner quality is evidence for cheating. Next, we turn to empirical data on mutualisms and highlight how our definition of cheating resolves much of the disagreement between the theoretical and empirical literatures on the prevalence of cheating.

A RE-EVALUATION OF THE EMPIRICAL EVIDENCE FOR CHEATING AND FITNESS CONFLICT IN MUTUALISMS

How common is cheating by mutualists in nature? A challenge of analysing the empirical literature is that empirical claims of cheating until now have been based on differing definitions of cheating. Armed with our relative-fitness-based definition, we critically re-examine the best-studied mutualisms. We note that these examples are representative but by no means exhaustive.

Ants and plants

Hundreds of plant species in the Asian, African and American tropics have convergently evolved domatia (structures that ants can live inside) and often also extrafloral nectaries or food bodies. These rewards attract ants, which defend the plant from herbivores or other enemies and thus increase plant growth. Larger plants provide more domatia and frequently more extrafloral nectar or food bodies to the resident ant colony, increasing ant colony growth (Frederickson & Gordon 2009). Since there is typically a single ant colony per plant, this positive feedback between plant and ant colony growth prevents 'investing less' in the partner from becoming a viable cheating strategy for either partner. However, several *Allomerus* and *Crematogaster* ant species, which are otherwise good defenders, exhibit a curious behaviour: they destroy flowers on their host trees (Yu & Pierce 1998; Stanton *et al.* 1999). This flower-attacking behaviour, variously called plant castration or sterilisation, severely reduces plant fecundity (Yu & Pierce 1998; Frederickson 2009; Szilagyi *et al.* 2009), but

increases plant vegetative growth to the advantage of the ants – more domatia enable larger, more fecund colonies (Frederickson 2009). Thus, these ants may have evolved to extract more benefits from their host plants via sterilisation. Surprisingly, this ant behaviour may not reduce plant lifetime fitness; a demographic model by Palmer *et al.* (2010) found that the sterilizing ant *Crematogaster nigriceps* actually increased acacia fitness by strongly promoting plant survival at the expense of reproduction until the acacias were colonised by other non-sterilizing ants and could set seed. However, whether sterilisation *per se* or other *C. nigriceps* traits are what promote acacia fitness remains an open question. Thus, whether or not plant sterilisation by ants qualifies as cheating depends critically on whether this behaviour reduces plant lifetime fitness, and the current evidence is equivocal.

Plants and pollinating seed consumers

Several groups of plants, notably figs and yuccas, are pollinated by insects that are also seed consumers (reviewed in Dufay & Anstett 2003). Since it is rare for all seeds to be destroyed (Janzen 1979; Keeley *et al.* 1984) and the plants often lack other pollinators, the pollinating seed consumers generally provide a net benefit to the plant. There are essentially two ways that the insects could cheat the plant: by pollinating less or by consuming more seeds. Non-pollinating fig wasp and yucca moth species have evolved from pollinating ancestors, but only rarely. In fig wasps, there are only two known non-pollinators nested within pollinator clades (Herre *et al.* 2008), among hundreds of described pollinating fig wasp species; additionally, very few individuals of pollinating fig wasp species fail to carry pollen (Jandér & Herre 2010). In yucca moths, there are two non-pollinating lineages nested within *Tegeticula*, which contains 14 pollinating yucca moth species (Althoff *et al.* 2006). However, it is not clear whether any fitness advantage is derived from neglecting to pollinate the host plant. It has been argued that the cost of pollination is small (Pellmyr 1997); meanwhile, pollination benefits the pollinator itself by increasing the chance that the fruit containing the pollinator's eggs will be retained and that there will be resources (seeds in yuccas and ovules in figs) for the maturing larvae to consume. Therefore, there is not conclusive evidence that the non-pollinators are cheaters. With respect to cheating by consuming more seeds, Herre & West (1997) suggested that higher oviposition rates could increase wasp fitness to the detriment to the fig. However, variation in the number of fig wasps that emerge from a fig is influenced by many factors, including the number of wasps that visit the fig, their behaviours inside the fig and the resources allocated by the tree to the developing fig. Therefore, though it is plausible that insects cheat by consuming more seeds, we are lacking data on whether this behaviour increases insect relative fitness and decreases plant lifetime fitness.

Plants and generalised pollinators

Almost all plants whose flowers are tubular or that have nectar spurs are exploited by nectar larcenists, animals that take nectar but that rarely or never transfer pollen (Irwin & Mal-

oof 2002). Nectar larceny can occur via (1) puncturing the flower to reach the nectar, (2) feeding through holes made by others or (3) entering the floral opening but not transferring pollen due to morphological mismatch (Inouye 1980). Although the behaviours of pollination and larceny are discrete, the distinction between cooperators and cheaters is surprisingly hazy. The floral visitor's behaviour can depend on the partner, as most animals that have been identified as nectar larcenists of one plant species are known to be effective pollinators of other plant species. The behaviour can also depend on the individual within the species, with some individuals acting as pure nectar larcenists and others behaving solely as legitimate pollinators. Finally, the behaviour can vary among visits; floral visitors commonly have multiple foraging behaviours within their repertoires (Bronstein 2001; Irwin *et al.* 2010) and almost any combination of mutualistic and non-mutualistic floral visitation behaviours can be found, sometimes on a single plant species (e.g. Richardson & Bronstein 2012). Nectar larcenists can have consequences ranging from negative to positive effects on the male and/or the female components of plant reproductive success (reviewed by Irwin *et al.* 2010). Depending on the system, these effects can occur through both direct mechanisms (e.g. by damaging floral reproductive organs) and indirect mechanisms (e.g. by leading pollinators to skip robbed flowers or to visit them only briefly). Thus, the fitness consequences of nectar larceny for the plants are sometimes, but not always, consistent with larceny being a form of cheating. In principle, floral visitors might gain fitness benefits by robbing instead of pollinating, but at present there are virtually no data available to evaluate this assumption.

Plants and arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) often benefit their host plant by increasing nutrient and water uptake in exchange for plant carbon. However, it is also fairly common to observe them reducing host plant performance (Hoeksema *et al.* 2010), especially under conditions of low light and/or high soil phosphorus (P) concentration (Johnson *et al.* 1997; Johnson 2010). Whether or not AMF cheat is a topic that has received a reasonable amount of attention in the last three decades (reviewed in Smith & Smith 1996; Johnson *et al.* 1997; Hoeksema *et al.* 2010). It remains unclear whether specific AMF strains always reduce performance of a particular host plant or whether their effects vary depending on the abiotic or biotic context. A study inoculating 10 plant species with each of 11 AMF strains found that each AMF had both positive and negative effects that depended on which plant species it was interacting with, while every plant species benefited from at least one AMF species and had reduced fitness in the presence of at least one AMF species (Klironomos 2003). Smith & Smith (1996) reviewed research on a particular strain of the arbuscular mycorrhizal (AM) fungus *Scutellospora calospora* that has been shown to provide little or no growth benefit to multiple plant species, and to demand more carbon and provide less P to its hosts compared to other AM fungal strains in the same studies. They conclude, however, that it is possible this potential cheater would be more beneficial to its hosts

under different conditions. Clearly, particular strains of mycorrhizal fungi can reduce host fitness relative to other strains and even relative to no partner under some conditions. However, the connection between a decrease in host benefit and an increase in fungal performance has only rarely been tested. Bever *et al.* (2009) showed that an AMF that provides little benefit had higher spore volume than a more beneficial AMF species when the two were well-mixed, suggesting that there is a cost to acting as a beneficial mutualist. Moreover, spatial separation of the two AMF reverses this outcome to favour the more beneficial AMF, implying that plants have mechanisms for regulating symbiont fitness that may prevent cheating, provided there is sufficient spatial structure in the symbiont community. Furthermore, Kiers *et al.* (2011) show that both partners have the ability to adjust resource fluxes in response to the amount of resources they receive. Finally, a study with four grasses found that plant species differ in their ability to reduce carbon allocation to low-quality AMF (Grman 2012). While this variation in stabilizing mechanisms could allow AMF to cheat, we largely lack coupled estimates of host and symbiont fitness to assess the prevalence of cheating in these interactions.

Legumes and rhizobial bacteria

Legumes form symbioses with soil-transmitted rhizobial bacteria in which photosynthetically fixed carbon is exchanged for symbiotically fixed nitrogen in root nodules; nodule size and nodule number are both fitness components of the rhizobial partner (discussed in Friesen 2012). Each partner might cheat by offering few or no resources while still accruing resources from the other, and there is substantial variation in plant growth with different microbial partners (Thrall *et al.* 2000; Friesen 2012). While a recent meta-analysis found overwhelmingly positive fitness correlations between legumes and rhizobia in single-strain inoculation experiments (Friesen 2012), three studies have found negative genetic correlations between nodule size and plant size (Laguerre *et al.* 2007), nodule number and fruit number (Heath 2010) and nodule size or number and seed number or size (Porter & Simms 2014); this suggests that there is sometimes fitness conflict between partners. However, in natural settings, multiple microbial strains can interact with the same host individual – these communities of symbionts on a single host mean that rhizobium–rhizobium interactions can have effects on fitness outcomes that are not captured by single-strain experiments. Less-beneficial symbionts could freeload on the mutualistic benefits generated by more beneficial strains (Denison 2000; Friesen & Heath 2013; Kiers *et al.* 2013). However, plants can preferentially direct rewards to better rhizobia and can also choose which strains to interact with (e.g. Heath & Tiffin 2009; reviewed in Friesen 2012), which could prevent low-quality partners from gaining a fitness advantage. One rhizobium strain that has been referred to as a cheater provides no nitrogen to the plant and proliferates in nodules (Sachs *et al.* 2010a), but forms few nodules when competing against beneficial strains (Sachs *et al.* 2010b). Furthermore, this strain is phylogenetically disjunct from co-occurring mutualistic strains (Sachs *et al.* 2010a) and thus did not arise within a population of mutualists as would

be expected if there was a fitness advantage of cheating. Another rhizobium strain does not cheat its host plant directly, but can exploit the benefits generated by a near-isogenic mutant strain when both colonise the same host by accumulating greater amounts of the storage molecule PHB (Ratcliff & Denison 2009; Kiers *et al.* 2013); however, this fitness advantage is only apparent at an early time point, and a game theoretical analysis suggests that this strain would not spread (Friesen & Heath 2013). Recent work demonstrates natural selection for rhizobium genotypes that decrease plant performance, but these experiments were conducted with only a single strain present and all strains in the natural population confer high benefits, so these strains must not prosper under normal circumstances (Porter & Simms 2014). Thus, outside of single-strain inoculation experiments that restrict the plant's ability to exert partner choice (i.e. Sachs *et al.* 2010a, b; Porter & Simms 2014), there are currently no unequivocal examples of rhizobial cheaters that increase their fitness by fixing less nitrogen.

Cleaners and clients

Cleaning mutualisms involve members of one partner species ('cleaners', typically fish and shrimp) that remove ectoparasites and other particles from partner species ('clients'). Cleaning results in improved hygiene for the clients, in one case with demonstrated fitness benefits (Waldie *et al.* 2011), and yields a meal for the cleaners. It is likely that cleaning mutualisms originated as by-product mutualisms (Barbu *et al.* 2011), and neither partner is expected to benefit by investing less in the interaction. Nevertheless, there is conflict between clients and some cleaners that actively consume client mucus, flesh or blood (Grutter & Bshary 2003). Although some cleaner species prefer ectoparasites (Barbu *et al.* 2011), the cleaner wrasse *Labroides dimidiatus* prefers client mucus over the most common ectoparasites (Grutter & Bshary 2003). When a client is bitten by the cleaner, it responds with an involuntary physical jolt; individual *L. dimidiatus* cleaners fall into a bimodal distribution of the number of jolts they induce in hosts. Biting cleaners were invariably females, and with one exception they only bit clients during spawning (Bshary & D'Souza 2005), when their food requirements are highest and the short-term benefits of feeding on client tissue may outweigh the long-term costs of alienating clients. In contrast, a related species, *L. bicolor*, consistently causes clients to jolt. Unlike its relative, *L. bicolor* roves over large areas and does not have repeated client interactions (Oates *et al.* 2010), which might otherwise provide an incentive to maintain cooperative behaviour. However, it is not known how costly it is for a client to be bitten, or how much of a fitness increase cleaners receive from biting their clients, so we cannot conclude that cleaners cheat without additional data.

How common is cheating?

Across these well-studied mutualisms, there is ample evidence of variation in the benefits provided to the partner and the benefits extracted from the partner. In both specialised and generalised pollination systems, there is variation in whether the flower visitors provide benefits by pollinating. Similarly, both mycorrhizae and rhizobia vary in how many resources they contribute to their host plants. Meanwhile, ants and cleaner fish vary in whether they perform behaviours that potentially harm their partners in order to extract greater benefits for themselves. Yet, despite all these observations, there is almost no evidence for the fitness costs and benefits necessary to establish conclusively that cheating is happening. In most cases, there is simply a paucity of fitness information, making it inconclusive whether the variation observed represents ongoing cheating. In the best-studied case of the rhizobia–legume mutualism, there is only evidence for cheating by some wild strains of rhizobia when the plant is prevented from choosing among multiple partners.

FUTURE RESEARCH DIRECTIONS

Moving forward, it is imperative that theoretical and empirical studies of mutualisms occur under a unified framework, so that data collected can be used in a predictive rather than a descriptive manner. We encourage empiricists to adopt the measurement framework outlined here, and we encourage theoreticians to explore additional real-world complexities of mutualism. To spur these activities, we outline challenges for future empirical and theoretical work. Meeting these challenges will require that the field move away from the binary 'cheater'/'cooperator' divide and embrace a quantitative perspective on mutualisms, the potential for fitness conflict between partners, and the consequences of this conflict.

Variation in partner quality: from genes to evolutionary processes

Recognizing that cheaters according to our relative-fitness definition may be absent from extant mutualisms due to stabilizing mechanisms leads to several urgent questions that can be approached using genetics. Identifying the genes underlying mutualistic traits can give insight into the evolutionary history of mutualisms, the mechanisms currently producing and maintaining partner quality variation, and the likely future evolution of the mutualism.

Once genes that contribute to partner quality and stabilizing mechanisms have been identified, comparative and population genomic approaches can be used to make inferences about the forces driving mutualism evolution. For example, did sanctions against uncooperative partners arise as innovations favoured by cheating, or are they exaptations that originally evolved to optimise resource allocation and that subsequently favoured the evolution of cooperation (Frederickson 2013)? Has there been balancing selection on mutualistic traits, as expected with negative frequency dependence, or stabilizing selection (e.g. Bailly *et al.* 2006)? Is there ongoing co-evolution between cheating strategies and stabilizing mechanisms, or have fitness conflicts largely been resolved (Foster & Kokko 2006; Frederickson 2013)?

Experimental manipulations could also take advantage of known genetic bases of mutualist traits. Individuals could be genetically engineered to enable precise manipulation of partner strategies. Manipulation of reward production and extraction traits would allow the fitness effects of strategy variation

to be measured without the confounding effects of overall genetic quality. Meanwhile, manipulation of partner fidelity and partner control mechanisms could help decompose partner quality into the contributions from each mutualist (analogous to the contribution of host and parasite to virulence; Casadevall & Pirofski 1999).

Finally, elucidating how the genes underlying variation in partner quality interact is necessary in order to develop predictive evolutionary models. The genetic nature of the trade-offs that generate fitness conflict can influence the trajectories of the evolutionary dynamics (Nuismer *et al.* 2003; Carter *et al.* 2005). Non-additive genetic architecture due to pleio-

tropy and epistasis can furthermore affect how quickly phenotypes are reached through evolution (Wade 2007), which may be particularly critical in populations at risk of extinction (Gomulkiewicz & Houle 2009).

Context dependency of strategies and outcomes: mutualisms in changing environments

The costs and benefits of mutualism are well known to depend on the abiotic and biotic environment (Bronstein 1994; Chamberlain *et al.* 2014; Box 4), but the mechanisms behind context dependency are only beginning to be under-

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Box 4 Measuring context-dependent fitness conflict and cheating

While fitness variation in mutualisms can arise from genetically (G) determined differences in traits that influence partner quality, interaction outcomes are often dependent on phenotypic plasticity in response to the abiotic environment and the community context of other partners that may interact simultaneously with a focal partner (E), genotype-specific responses to the environment (G × E), and non-additivity between partner genotypes (G × G), which may also depend on the environment (G × G × E). Furthermore, in multi-partner interactions there could be cheating by freeloading if the focal partner is unable to direct rewards to cooperators rather than freeloaders. Due to these different forms of context dependency, assigning a single measure of partner quality for a particular genotype is often not possible, or more precisely is only valid in a particular abiotic and biotic environment and for a given partner. More complex experimental designs are required to properly account for context dependency when assessing cheating.

Environmental context dependence and phenotypic plasticity: Some variation in performance can always be expected from the environment (E). The environment can affect an individual's overall physiological state and ability to invest in its partner. The environmental context may also affect the costs and benefits of mutualist rewards themselves, such as a lack of benefit to protection mutualists if there are no enemies present. Mutualism traits can also respond plastically to the environment, such as legumes' ability to down-regulate nodulation and mycorrhizal colonisation under high soil nutrient levels. In many cases, there is also genetic variation in phenotypic plasticity, with genotypes having different responses to the environment (G × E).

Non-additive cross-species genetic effects: There is significant evidence for epistatic genetic interactions between the genotypes of partners (G × G), with some genotypes only providing a benefit to specific partner genotypes. The best examples of these interactions come from the legume–rhizobia and plant–mycorrhizal literature, which typically find evidence of genetically based compatibility. The same strain of rhizobium may be highly beneficial on some host genotypes but be a low-quality partner on others (e.g. Thrall *et al.* 2000; Heath 2010; discussed in Friesen 2012), and rarely a generally beneficial strain may be parasitic on particular genotypes (e.g. Laguerre *et al.* 2007). Similarly, the same strain of mycorrhizal fungus can be beneficial to one plant genotype but parasitic on another (e.g. Johnson *et al.* 1997; Grman 2012), with further non-additive effects of the environment (G × G × E; e.g. Piculell *et al.* 2008).

Communities of mutualists – multi-partner interactions: In many mutualisms, a focal individual will interact with multiple partners. Especially when these interactions are simultaneous (e.g. a legume with many rhizobia), another form of cheating might occur: freeloading on the benefits generated by other members of the guild that are more cooperative. Freeloaders are cheaters only when they co-occur with cooperators, since they rely on cooperators to induce reward production by the shared host. To detect cheating by freeloading, fitness must be measured in multi-partner experiments against a background that reflects the population distribution of other partners.

Experiments needed to identify context-dependent cheating: In order to account for context dependency in bipartite interactions, single partner genotypes must be paired factorially across an environmental gradient. Standard variance decomposition methods can then be used to estimate the effects of G, E, G × E, G × G, and G × G × E on each partner's fitness (e.g. Heath 2010; Porter & Simms 2014). Genetic correlations can be estimated within this statistical framework to determine whether there is fitness conflict within the interaction (e.g. Heath 2010; Porter & Simms 2014).

In multi-partner interactions, an informative experimental design would be to vary the relative frequency of a focal partner in a mixed community. If the relative frequency of the focal partner increases after the interaction, we would infer that it has higher relative fitness than other partners. If, furthermore, the host's fitness decreases with increasing frequency of the focal partner, we could infer that the partner is indeed a cheater. In the legume–rhizobia mutualism, the opposite pattern was found: some rhizobium strains increased in frequency after multiple passages through symbiosis with *Medicago truncatula*, but these strains gave the highest host fitness in single-strain interactions, consistent with effective partner choice that could disfavour cheating (Heath & Tiffin 2009).

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stood. Environmental change intensifies the need for a mechanistic understanding of how the environment affects both the expression of mutualism traits and the relationship between mutualism traits and fitness.

To predict mutualism performance and evolution in changing environments, we must develop mechanistic models that connect the physiological and ecological dimensions of the interactions to fitness. We first require data on the costs and benefits of mutualism in the context of specific environments; furthermore, these costs and benefits should be considered relative to alternative methods of obtaining rewards (e.g. Hoeksema & Schwartz 2003). Environmental quality, as well as the presence or absence of antagonists or alternate mutualists, may affect whether rewards are needed, how readily available rewards are from different sources and how costly rewards are to offer.

Environmental change may in fact facilitate the acquisition of a mechanistic understanding of mutualistic interactions in two ways. Our conceptual framework suggests that cheating and fitness conflict are most likely to be detected away from evolutionary equilibrium. Thus, sources of fitness conflict could be revealed by studying mutualisms that are currently responding to environmental changes or to novel partners (Mayer et al. 2014). Environmental perturbations also enable tests of the role of the environment in mutualism evolution. Theory predicts that the potential for conflict between partners increases with environmental quality, since the relative importance of the partner decreases (Hochberg et al. 2000). Some contemporary changes have led to increased environmental quality. For example, modern agriculture has bred crops that perform well in high-nutrient environments, which can decrease their ability to interact with nitrogen-fixing symbionts. In the case of soy, older cultivars obtain more benefit from a mixture of rhizobia strains than newer cultivars, which suggests the decay of host mechanisms that align partner fitness (Kiers et al. 2007). Meanwhile, rhizobia in a long-term nitrogen addition experiment evolved to be less beneficial to their legume host plants (Weese et al. 2015). Other types of global change cause increased stress, such as heavy metal contamination, higher temperatures and increased or decreased precipitation (Kiers et al. 2010); it remains to be tested whether these stressors increase the importance of mutualist partners and thus fitness alignment, as predicted by theory, or whether their importance is decreased.

Multi-modal interactions: a pluralistic approach to mutualism

We have emphasised that an individual's partner quality depends on both how much reward it provides and how much reward it extracts from the partner. However, most models focus on only one dimension of the interaction – the amount of reward produced. Therefore, many theoretical questions remain about how traits affecting reward extraction evolve and what mechanisms can curb cheating along this alternate path. Fixation on the idea of cheating as investing less in the partner may also have led to the neglect of other potential forms of cheating in empirical investigations.

Currently, theoretical predictions about cheating derive mostly from cheating as giving less reward; we know very little about other aspects of partner quality or the relationships among partners along additional trait axes. Although some evolutionary models incorporate two modes of interaction [e.g. cleaning and biting of client fish (Poulin & Vickery 1995; Johnstone & Bshary 2008); pollination and seed predation (Law et al. 2001; Jones et al. 2009)], there has been almost no exploration of variation in two modes simultaneously (but see Ferdy et al. 2002). There has also been no direct comparison made between different forms of cheating. In particular, theoretical studies could determine whether types of cheating differ in the threat they pose to the persistence of mutualism and the mechanisms needed to oppose them.

Future empirical studies investigating conflict in mutualism should measure the control that each partner has over each step in the production and consumption of the rewards exchanged (Fig. 5a). Such studies are necessary in order to determine whether cheating is occurring through routes other than producing less reward. In particular, we expect that conflict over reward consumption may be common in mutualisms derived from host–parasite interactions. In these mutualisms, former parasites have evolved to benefit their hosts; however, they may not have completely lost the original parasitic traits used to extract benefits from their hosts. Studies of this nature should also consider whether or not different types of conflict over reward exchange are stabilised by the same mechanisms.

The scope of both theoretical and empirical studies on cheating and conflict should also be broadened beyond the resources and services traditionally recognised as mutualism rewards. There are a growing number of examples of conflict between partners over other aspects of the interaction. For example, there can be conflict between plants and their fungal endophytes over pollen vs. seed reproduction and seed dormancy, with endophytes manipulating these life-history traits to increase their transmission rate (Afkhami & Rudgers 2008; Gorischek et al. 2013). In addition, figs and fig wasps may experience conflict over wasp sex ratio, as male wasps do not provide any benefit to the fig (e.g. Herre et al. 2008). Thus, even if the primary rewards exchanged between partners exhibit fitness alignment, there may be traits for which fitness conflict arises from different trait optima for each partner.

CONCLUSION

Although cheating is currently held to be an important facet of mutualism, the claims of cheating in empirical systems are based on disparate definitions of cheating. To move forward as a unified field, we must adopt a common theoretical and empirical framework for investigating cheating and fitness conflict in mutualism. We propose that cheating can be defined as increasing the fitness of the actor above average fitness and decreasing the fitness of the partner below average partner fitness. This definition focuses on fitness outcomes rather than on specific strategies employed by mutualists, since only fitness outcomes are informative about the evolutionary threat to the mutualism. Adopting a fitness-based definition will reinforce the idea that the concept of cheating applies to a wider range of phenomena than just investing less in the partner, including extracting more benefits from the partner. Moreover, unlike previous fitness-based definitions, our relative-fitness definition specifies the comparison needed to

test for cheating. Standardizing the measurement of cheating will facilitate comparisons between systems and enable a critical assessment of the degree of fitness conflict in mutualisms. Expanding mutualism theory to encompass a greater degree of biological realism, particularly multi-modal interactions, will pave the way to empirically parameterised mechanistic models. These models will be crucial as we seek to predict the consequences of cheating and conflict on mutualism ecosystem services under changing environments. Such models will also provide the ultimate test of our understanding of mutualistic interactions.

AUTHORSHIP

EIJ and MLF co-organised the NCEAS working group that led to this paper, wrote sections of the first draft and assembled and edited the manuscript. All other authors contributed substantially to discussions leading to the conceptual framework described here, writing sections of the first draft and revisions of the manuscript.

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