Unexplained Cooperation

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Abstract.
Social evolution theory provides a wide array of successful evolutionary explanations for cooperative traits. However and surprisingly, a number of cases of unexplained cooperative behaviour remain. Shouldn't they cast doubt on the relevance of the theory, or even disconfirm it? This depends on whether the theory is akin to a research programme such as adaptationism, or closer to a theory – a set of compatible, (dis)confirmable hypotheses. In order to find out, we focus on the two main tenets of social evolution theory, namely reciprocity explanations and kin selection. Reciprocity-based explanations are extremely hard to (dis)confirm. This is due, first to the multiple realisability of explanatory processes, factors and strategies, despite apparent reasons to the contrary; second, to the high quantity, and limited availability of data needed to eliminate or back up such explanations. One of our target cases vividly illustrates these limitations. Moreover, kin selection, while relatively easy to disconfirm in particular cases, seems to enjoy a more limited explanatory scope than previously thought. Overall, social evolution theory turns out to be neither a research programme nor a theory, but a heterogeneous scientific entity, composed of parts that are amenable to (dis)confirmation and others barely so.

1. Introduction

About sixty years ago, there was no social evolution theory. Cooperative traits – behavioural traits such their bearers benefits when they interact – and among them, altruistic traits in particular – beneficial to others but costly to their bearers – had received no satisfying explanation. Nowadays though, social evolution theory is thriving. Within In particular, among social behaviours, countless cases of cooperative behaviours may now be explained in terms of kin selection, direct or indirect reciprocity, group selection, greenbeards, lateral gene transfer, about which recent works abound.[1] Even the fair number of controversies it recently witnessed have displayed its good health rather than threatened it (as we will see).

All this is well known. It may thus come as a surprise that there are cases unexplained cooperative behaviours – instances of cooperation that are problematic given the existing theoretical background. In this

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[1] See for instance, only in the last decade or so: Tomasello 2009, Bourke 2011, Gintis & Bowles 2011, Sterelny et al. 2013, Marshall 2015, Birch 2017.

paper, we aim, first, to describe and characterise these cases, and second to assess their consequences for social evolution theory. Do they point to possible shortcomings of social evolution theory or are they just cases awaiting theoretical integration?

Depending on the answer to this question, consequences can then be drawn about social evolution theory itself. It may, not unlike adaptationism itself, not be amenable to (dis)confirmation and so not be threatened by problematic sense. If, however, it is more similar to a theory, that is, to a set of testable hypotheses, then such cases may prove worrying. As we will see, there are reasons to doubt both views and to see social evolution theory as a heterogeneous scientific entity, confirmation-wise: although some of its parts are vulnerable to empirical counterexamples, others hardly are.

Our argument unfolds as follows. Section 2 recalls the main features and the explanatory success of social evolution theory. Section 3 describes four cases of problematic, unexplained cooperative behaviour and identifies their common features – namely that they escape kin selection and are only speculatively compatible with reciprocity-based explanations. Section 4 discusses reasons why social evolution theory may be thought as vulnerable to empirical counterexamples in principle, in contrast to adaptationism in general. The following two sections then discuss the main two tenets of social evolution theory and pave the way for our final diagnosis. Section 5 discusses in detail one particular case of cooperative behaviour (cooperative courtship in long-tailed manakins), which helps highlight how difficult confirming or disconfirming reciprocity-based explanations is. Section 6 focuses on kin selection, which, though empirically vulnerable, has seen its explanatory scope threatened. As a consequence, the relative scope of–and problems associated with–reciprocity explanations increase. Section 7 then clarifies the status of social evolution theory from a confirmatory perspective. After discussing what makes it different from both a research programme and a theory, we will argue that it is neither. Social evolution theory should be seen as a heterogeneous unit, a confirmatory patchwork. Overall, the existence of cooperative behaviours for which we do not yet have explanations is not a sign of weakness.

2. Social evolution theory

The purpose of social evolution theory is to explain the evolution of social traits, that is, traits that are beneficial or costly to individuals other than their bearer. It mostly focuses on cooperative ones. Cooperation refers to behavioural traits from which their bearers benefit when they interact. Among cooperative traits, mutualistic traits are beneficial both to their bearers and to others. By contrast, altruistic traits benefit others but are costly for their bearer.[2] Accordingly, the main purpose of the theory is to solve the problem of cooperation posed by the latter traits, which can be formulated in this way: why should a behavioural trait that benefits others but is potentially costly to its bearer be enhanced by natural selection?

Rather than a unified theory, social evolution theory is best understood a set of distinct explanatory principles, such as kin selection (Hamilton 1964), group selection in its 'old' and 'new' forms (Wynne-Edwards 1962, Wilson 1975, Maynard-Smith 1976), direct and indirect reciprocity (Trivers 1971, Alexander 1987) as well as other mechanisms such as green beards (Dawkins 1976, Gardner & West 2009) and lateral gene transfer (Birch 2014).[3] These principles may in turn lead to one or several more specific hypotheses regarding any given cooperative trait.

At the highest level of abstraction, all explanations of cooperative behaviour share one property: they involve positive assortment (Fletcher & Doebeli 2009; though there may be rare conceptual exceptions, as suggested by Archetti & Scheuring 2012). In all existing explanations, cooperators end up more likely to interact with other cooperators for one reason or another; and as a result, cooperators benefit more from cooperative efforts than non-cooperators do. So we could say there is only one general explanatory scheme for cooperative behaviour-one explanans for one explanandum. However, this would be overselling the simplicity of the theory. For each explanatory principle can in turn be individuated at a finer grain–it is compatible with various mechanisms, which are multiply realisable (as we will see below in section 4.2). Even if cooperators always need to preferentially interact with other cooperators for cooperation to evolve, the ways in which this preferential interaction is realised, and the various characteristics of what counts as a cooperative agent, make the explanatory principles quite distinct. Moreover, as we will also see, the various principles do not behave similarly when it comes to the search for possibly conflicting evidence. Overall, SET is a strange, layered beast: a set of explanatory principles, each of which may allow for numerous specific hypotheses regarding the evolution of a cooperation trait.

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[2] Here and throughout this paper, benefits and costs are to be understood in terms of biological fitness, as is customary in evolutionary biology. Additional relevant social traits are spiteful and egoistic traits, which are costly for other individuals and respectively costly or beneficial for the bearer.

[3] A number of these principles are often called theories as well, e.g. kin selection theory of reciprocity theory. However, to avoid confusion, throughout this paper we reserve the term 'theory' to SET.

All explanatory principles for cooperative behaviour share another feature though: they do not solve the problem of altruism, but rather dissolve it: what appears individually costly at first sight turns out to be beneficial in some way. For instance, in kin selection, apparently altruistic behaviour actually furthers the spread of altruistic genes shared by the individual's parents–individual fitness costs are compensated by fitness benefits of genetically similar individuals. In reciprocity theories, one's apparent fitness cost turns out to be illusory when considered in the long term, when additional benefits accrue. All explanations of cooperative behaviour similarly identify hidden fitness benefits[4] that compensate for the apparent individual costs, one way or another.

The success of this explanatory strategy has been nothing short of striking. SET has displayed great flexibility and proved able to integrate new factors associated and correlated with cooperation or by taking into account new kinds of agents. As far as we know, most apparently problematic or surprising factors associated with cooperative behaviours have been explained away. Let us briefly mention a few recent ones. Several possible mechanisms link monogamy with cooperation: kin selection, but also ecological and hormonal factors (Dillard & Westneat 2016). Aquatic environment has an influence on the evolution of cooperation and is basically explained by kin selection. It offers one way in which physical dispersal, which decreases competition between kin, can be realized (Bourke 2011). When it comes ot agents, social evolution theory covers cases of cooperation on a lower scale than individuals, since it explains, for instance, the evolution of the sociality of sperm cells, bacteria, or transmissible cancer cells. Sperm cooperation is broadly explainable by kin selection (Foster & Piazzari 2010). Cancer cell cooperation is explainable by evolutionary transition mechanisms, which, although the object of much current research, are better and better understood (Bourke 2011, Laplane & Germain 2017). Finally, lateral gene transfer has only recently been recognized as having explanatory import for the evolution of bacterial sociality (Birch 2014).

In short, so far SET has successfully integrated possibly worrying cases, which can thus legitimately be seen as mere puzzles, that is, as solved or solvable through slight extensions or modifications of the theory.[5] These cases typically become part of the regular scientific activity and do not raise specific explanatory issues. This makes the

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[4] Which may accrue to various entities, whether they be individuals of the target population, their genes, groups of them, etc.

[5] One may be tempted to call them Kuhnian puzzles, but we do not want to commit to the view that SET is a paradigm. Similarly, when we talk of anomalies below, we only mean case that resist integration under any of the explanatory principles that jointly constitute SET.

existence of genuinely unexplained cases of cooperation, to which we now turn, all the more surprising.

3. Unexplained cooperative behaviours

This section introduces four cases of unexplained cooperation, all of which will share similar features, as we will see.

Like for many other species, the mating system of long-tailed manakins (*Chiroxiphia linearis*) involves a courtship period, during which males, who belong to a hierarchically organised group, sing and dance in front of females that are visiting their lek arena (the zone controlled by the group; McDonald & Potts 1994, Trainer et al. 2002). Less typical is the fact that the court display is always cooperative: two males actually sing a duet and dance jointly–usually an alpha and a beta male. Now comes the interesting part: only the alpha males then proceed to mate with a visiting female, which renders the behaviour of the beta male puzzling. Moreover, beta males assist alpha males for long periods–up to ten years. Alpha and beta males are usually unrelated; and possible direct future benefits that accrue to the beta male are difficult to identify. McDonald & Potts (1994) mention four (related) such possible benefits: beta males may still sometimes mate with females, although rarely; they may succeed the alpha male when needed (which increases their mating prospects); females may exhibit fidelity to a lek arena even when alpha males change; and beta males may contribute to the high reputation of such an arena. However, whether such benefits are sufficient for the assisting courtship behaviour to become an adaptation, especially given the delay they involve, remains unclear.[6].

Meerkats (*Suricata suricatta*) live in groups of up to 25 individuals, with a dominant female. Like many other social species, they raise their pups cooperatively: pups can be fed by any female member of the group. In similar species, cooperative rearing is usually performed by family members, and is thus explained by kin selection. However, in the case of meerkats, the level of rearing help is not correlated with the helper's degree of kinship with the pups (Clutton-Brock et al. 2001), unlike in other species such as naked mole-rats or brown hyenas. Here, a typically explainable behaviour turns out to be explanatorily puzzling. However, an alternative hypothesis to kin selection is possible. Group augmentation could explain cooperative rearing in the absence of kinship, or could work in combination with kin selection (Kokko

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[6] But see Edelman & McDonald 2014, discussed in section 7.

et al., 2001). This might explain why individuals have an increased fitness in larger groups. For example, in meerkats, the larger the group size, the higher the fitness, as this helps to protect the group from predation (Kingma et al. 2014). The group augmentation hypothesis may be based on mutual benefits, or on reciprocity mechanisms.

In Stillwater, Oklahoma, American crows (*Corvus brachyrhynchos*) manifest unusual breeding behaviours–they typically delay their reproduction despite the abundance of partners and of available nesting spots–and dispersion patterns–unrelated crows often circulate between nests in order to participate in cooperative breeding (Caffrey & Peterson 2015). Moreover, these nest immigrants are easily accepted and trigger little aggressive reactions. Here again, kin selection offers no explanation; neither do reciprocity theories. Furthermore, many of Emlen's (1995) predictions, based in part on kin selection, do not apply well to the observations made by Caffrey and Peterson. For instance, contrary to one prediction, sexual aggressions did not occur more frequently in groups of non-relatives than in group of relatives. Concerning breeding behaviours, potential benefits are elusive, such as that of getting to know ones territory or potential future partners better, and it is difficult to see how they could counterbalance the fitness loss caused by years without reproduction.

Common warthogs (*Phacochoerus africanus*) too are cooperative breeders. However, far from being systematic, their breeding behaviour is highly variable (White & Cameron 2011). Some females raise their pups in isolation, others in groups; babysitting, adoption and non-offspring nursing behaviours are sometimes observed and sometimes not. Moreover, such breeding strategies seem context-dependent; for instance they appear to vary with the individual's age and with seasonal differences. Here again, kin selection explanations are not available, and reciprocity mechanisms remain tentative.

These four examples do not exhaust all cases of unexplained non-human cooperative behaviours.[7] However, these share a number of interesting features. First, they concern widespread traits in non-human animals, namely courtship displays and breeding. Second, none of them appear to involve kin selection, although it has long been considered as explaining most cases of cooperative breeding in vertebrates, for instance.[8] Third, all feature speculative scenarios of reciprocity-based

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[7] Such puzzling cases may be multiplied: the cooperative hunting behaviour of Malagasy fossas, which are otherwise solitary carnivores (Bekoff et al. 1984, Lührs & Dammhahn 2010); the collective suicidal punishment of leaf-cutting ants (Rissing et al. 1996); the pheromone-based recruitment of *Cataglyphis floricola* ants, which is unique among an otherwise non-recruiting genus.

[8] Mumme (1992) provides a famous example.

mechanisms with little empirical support. Indeed, reciprocity (often in its direct version) is the most widespread fall-back explanation for cooperative breeding when kin selection does not work (Clutton-Brock 2002). Overall, these case of unexplained cooperative behaviour do not appear too deeply problematic. Is this reaction (or lack thereof) legitimate?

4. The possibility of disconfirmation

4.1. SOCIAL EVOLUTION THEORY AND ADAPTATIONISM

We have presented a number of examples of cooperative behaviour, none of which is properly explained by social evolution theory (SET). All escape kin selection, and all are thought to be possibly captured by reciprocity-based explanations, the details and plausibility of which remain speculative. What are we to make of them? Should we see them as superficially problematic, which we should expect to be solved by SET reasonably soon, or as worrying cases that may threaten the explanatory scope of SET?

The former option seems to be favoured by the authors of the studies described in section 2, for whom our cases hardly qualify even as would-be anomalies, and who do not raise any negative conclusion regarding SET. Rather, they introduce speculative explanations, discuss their plausibility and shortcomings, but without drawing general consequences for our traditional understanding of cooperative traits. Our cases are just not seen as threatening the usual explanatory framework.[9] Rather, they are considered as intriguing cases to be solved. What we want to ask is whether it should be so, or whether social evolution theory is so entrenched that little doubt about it may emerge at all.

This problem may be deemed as too cliché in philosophy of biology to deserve attention. Since the early days of the theory of natural selection, adaptationist hypotheses have been criticised for being difficult or even impossible to falsify (Gould & Lewontin 1979). So maybe our cases of unexplained cooperation may not constitute anomalies for the simple reason that anomalies regarding adaptationist hypotheses, although

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[9] Of course, it would be unreasonable to claim that none of our cases is deeply worrying or has reached the status of an anomaly, for they are too recent. Our point is that they do not even seem to appear as would-be anomalies. Still, whether they could become collectively worrying, when taken together with the additional cases mentioned in footnote 7 above, remains speculative. As the examples are scattered across species, journals and years, they may simply never have been brought together by anyone.

possible in principle, are rare to begin with.[10]. The non-problematic status of yet unexplained cooperative behaviours would stem from its endorsement of an adaptationist perspective.

This characterisation of adaptationism turns on a straightforward distinction regarding the nature of a theory. Some scientific theories are sets of specific, testable hypotheses and as such are open to (dis)confirmation. Other theories are research programmes (Lakatos 1970), which involve a theoretical core that is impervious to (dis)confirmation and a set of auxiliary hypotheses that may be modified or abandoned on empirical grounds. One possible defence of SET against worrying cases could just argue that just like adaptationism, it is a research programme, that is, an entity that cannot be (dis)confirmed but rather judged according to its explanatory scope or problem-solving success rate (for instance).

However, the claim that SET is impervious to (dis)confirmation, or at least as impervious as adaptationism itself is, neglects at least three peculiarities of social evolution theory. First, SET targets one kind of phenomenon as its explanandum, namely social traits – those that affect fitnesses of entities, either in a beneficial or a costly way. Because of this restriction in the range of phenomena to investigate, we may expect the search for explanatory anomalies to be easier. This peculiarity is not decisive though, as in principle, adaptationism may work as a research programme even if it only targeted a handful of traits, by always refining evolutionary scenarios for their appearance, and because any research programme has a limited domain. However, note that our claim is comparative: because the scope of SET is more restricted than that of adaptationism, it should be easier to investigate its explanatory success and harder to justify its failures about some traits by resorting to possible future successes regarding other traits.

Second, as we have also seen, SET is constituted by a finite array of explanations schemas. As we have seen, there are only so many evolutionary mechanisms that may explain cooperative behaviours: kin selection, group selection, direct or indirect reciprocity theories, interacting structures, greenbeards, lateral gene transfer. This means that for any cooperative trait, there is a small list of usual explanatory suspects to check before we can start labelling it as a problematic case. In principle, explanatory options for the evolution of a given cooperative behaviour could thus be browsed and checked exhaustively.[11]

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[10] As is well known, there are good reasons to think that adaptationism in itself is not falsifiable; but adaptationist hypotheses, or at least good ones, are falsifiable in principle (Sober 2000).

[11] This is not to say that the list of candidate explanatory mechanisms cannot evolve. Indeed, we have witnessed a historical inflation of possible explanations during the last five or six decades, the last addition to which is lateral gene transfer as

By contrast, the variety of adaptationist hypotheses that may explain an arbitrary trait display no such limitations – this absence of constraint on adaptationist options is indeed what makes adaptationism a research programme or strategy, rather than a hypothesis that may be confirmed or disconfirmed. Social evolution theory covers traits that share specific characteristics, for which only a handful of possible evolutionary mechanisms may allow. So at first glance, that cases of unexplained cooperation do not constitute worrying cases is more puzzling than it would be in the context of adaptationist thinking in general.

A third reason why we may not want to treat adaptationism and social evolution theory on a par with regard to their empirical vulnerability is that the latter often targets a type of costly traits[12]. A common feature of cooperative traits is that they are also altruistic, that is, they provide a benefit to others at a personal cost (where benefits and costs concern fitness). For sure, other cooperative traits–mutualistic ones–involve no such cost. Still, in social evolution theory, the focus has historically been (and still is) on seemingly altruistic traits.

Here our point is this: when a trait is costly, natural selection should tend to make it disappear. As a consequence, that such a trait has reached fixation or at least has become widespread begs for an explanation. In such cases, there are good prior reasons to search for adaptationist hypotheses, because processes other than natural selection (for instance drift) would be less likely to have efficiently counterbalanced the evolutionary cost of altruistic traits. In short, it is more legitimate to favour adaptationist hypotheses in the case of costly traits. This is what has led theorists to keep suggesting adaptive explanations for the evolution of seemingly crippling traits (typically explained by sexual selection) or of sexual reproduction (which halves an organism's fitness as compared to asexual reproduction; see Ridley 2004, chap. 12). The succession of hypotheses supposed to explain such traits is thus not a sign of a loosely constrained research programme, but of a particularly intense explanatory motivation.

If these three arguments are sound, then SET seems distinct from an adaptationist-like research programme and closer to being a set of spe-

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relevant for bacterial sociality. Note that this does not mean that bacterial sociality was considered as a worrying case before, because some of it was partially explainable by other mechanisms (e.g. classical kin or group selection). Moreover, the conceptual role of lateral gene transfer turns up to be very similar to existing ones; it can even be formalised similarly to kin selection (that is, using and slightly modifying Price equation; see Birch 2014b).

[12] Among social traits, costly traits include altruistic and spiteful ones–both are costly to their bearers, and respectively beneficial or costly to others.

cific hypotheses – a theory – and thus amenable to (dis)confirmation. As a consequence, the puzzling cooperative traits described in section 2 should indeed be worrying. However, we now turn to reasons why this is not so.

4.2. THE MULTIPLE REALISABILITY OF COOPERATION PROCESSES

As we just saw, social evolution may encounter more anomalies than adaptationism in general, because of the unicity and frequent evolutionary cost of its explanandum, as well as of the small number and similarity of its classical explanantia. But does this entail that the theory of cooperation is likely to face worrying cases? Not quite.

Explanations of cooperation can be divided up in different ways. In section 2, we saw that the general explanatory scheme of positive assortment can be realised a number of mechanisms (kin selection, reciprocity theories, etc.). But further subdivisions are possible. Reciprocity-based explanations include direct and indirect reciprocity mechanisms. Moreover, explanations based on image scoring (Nowak & Sigmund 1998), biological markets (Noë & Hammerstein 1995) or policing (Frank 1995) highlight different mechanisms, even if all amount to a kind of reciprocity. Similarly, there are different kinds of group selection (whether the traits favoured by selection are possessed by individuals or collectives; see Okasha 2006), and of kin selection (which can act via subsocial or semisocial pathways, depending on whether relatives of different or of identical generations associate; see Bourke 2011).

The subdivision deepens, because any given mechanisms is typically multiply realisable in concrete situations. For instance, kin selection-based explanations apply when individuals interact preferentially with their kin. But how is this preferential interaction realised? Classically, individuals may be able to recognise their kin (for instance from their smell, look, etc.); but they may also happen to interact with them due to some of their specific features (for instance with limited dispersal, when parents happen to live close to their progeny). Cooperation typically evolves by indirect reciprocity when individuals recognise cooperative or non-cooperative partners they have never interacted. But such recognition may be multiply realised: by remembering past observed interactions between third parties; by detecting hints regarding the past cooperative or non-cooperative tendencies of possible partners.[13]

Even given a list of the relevant factors for the evolution of a cooperative traits, different combinations of such factors (and of the values of the parameters that represent them) may typically constitute a prima

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[13] For instance, song sparrows infer that close individuals are non-cooperators by listening to their intrusions on a neighbouring territory; see Akcay et al. (2010).

facie plausible explanans. This is particularly discernable in model and simulation-based approaches of cooperation, which focus on the equilibria of evolutionary systems–their possible stable endpoints and on the formal conditions which allow for the evolution of many traits, among which cooperative ones. In such approaches, traits can often evolve for a variety of parameter values (within models) or of relevant factors (across models). Such results multiply the number of possible ways in which cooperation may evolve, and so the number of possible explanations to take into consideration.

Another way to put this point is that any evolutionary explanation of a given trait is of the historical type; this allows for the crucial role of contingent, low-probability events. Model-based approaches of the evolution of cooperation tend to emphasise robust explanations – explanations which hold for a variety of models, or a variety of parameter values in a given models, to repeat. But the explanation of one particular trait does not have to be plausible: truth does not have to be robust (Woodward 2006). The contingent, local dimension of evolutionary explanations further increases the list of possible scenarios.

Finally, the range of possible explanations for a cooperative behaviour further increases because of the variety of scales at which the analysis may focus. A simple behaviour (a single action, say) need not have evolved in isolation. As rightly emphasised by Birch (2017: 26-8), the target of natural selection may be strategies, or pattern of behaviours. That is, it may be not a single action but that a sequence of possible actions (or a way to generate them) that has been selected. Consider for instance the famous tit-for-tat strategy: here, as with many strategies in repeated games, it is not the cooperative action alone that may be selected, but a set of rules saying when to cooperate and when not depending on what the partner does. As a consequence, an apparently cooperative action may be explained as being part of a general strategy; as there are many possible strategies in which a given action may feature, the set of possibly relevant evolutionary scenarios further balloons.

Overall, cooperation can evolve from different abstract mechanisms, which may be realised by different causal processes, concern various behavioural scales and depend on various factors, which are in turn multiply realisable and context-dependent. The prima facie limited number of cooperative traits and of available explanatory schemes only marginally reduces that of possible specific hypotheses. We now turn to an example that illustrates the difficulty of empirically confirming or disconfirming such hypotheses.

5. Reciprocity: the case of long-tailed manakins

How difficult is it to disconfirm, or even eliminate possible explanations of a given cooperative behaviour? Let us return to one of the cases described in section 3 and to a related attempt to confirm a reciprocity-based explanation, which will reveal how difficult disconfirmation can be.

The study of long-tailed manakins, *Chiroxiphia linearis* (Mc Donald & Potts, 1994), illustrates the difficulty of confirming (and indirectly, of disconfirming) potential hypotheses. As mentioned above, the behaviour of beta males towards alpha males does not appear to be a matter of kin selection or reciprocity. In order to successfully disqualify the possible influence of kin selection, the authors conducted genetic tests on a sample of 33 cooperative males, based on repetitive DNA (more exactly, polymorphic microsatellite loci). The aim was to measure the degree of kinship between beta males and alpha males; this was a relatively feasible task, and kin selection was thus out of the picture.

By contrast, consider a more recent study (Edelman & McMcdonald, 2014) on the same species. The authors study six possible patterns of interaction for the cooperative behaviours observed among manakins, four of which end up confirmed, based on: spatial proximity, social status, the 'friend of a friend' effect or triad closure effect, and finally the persistence of a link. The first pattern involves spatial proximity between birds: the males who display at neighbouring leks are more likely to cooperate. Social status may also play a role, since the probability of cooperating in the courtship increases with social status. The highest ranked males in the group hierarchy will find partners more easily and can therefore engage in more courtship parades. The third pattern corresponds to the fact that two individuals with a common social partner are more likely to become partners in turn. Finally, pre-existing and stable relationships appear to promote cooperation between males. Two other local patterns are also investigated but rejected as irrelevant: selective mixing (the fact that males could be more likely to cooperate with individuals of similar status) and preferential attachment by degree (whereby males with many partners for cooperation gain more cooperative partners).

The authors of this study use a technique called exponential random graph (ERG) to model and analyse cooperation networks among manakins. They start by constructing networks of observed interactions in which individuals are linked whenever they have actually cooperated in a mutual display. The study took place in Monterverde, Costa Rica, was described in several prior publications (McDonald 1989, 2010) and conducted on 139 colour-banded males between 1983 and 1998. The data was obtained from 2-year time intervals over this 14-year study period, for a total of 9288 hours of observation.

The authors then repeatedly generate by computer simulations model networks in which individual interaction stems from the six possible factors. They compare the goodness of fit of the model networks with the actual networks; when high enough, they remove the factor that least reduces this goodness of fit. The fit is deemed good enough as long as the similarity with respect to three metrics[14] between the actual and the simulated networks is high enough, that is, whenever the measured values of the actual network remain between the lowest and highest bounds obtained in the simulated networks. The fit is good in this sense until two factors (positive selective mixing and preferential attachment), but not more, are removed; hence the conclusion that link formation is 'largely explained' by spatial proximity, social status, triad closure and link persistence, while preferential attachment and selective mixing, '[does] not consistently explain the structure of male cooperation networks' (Ibid.: 125).

As a preliminary remark, note already that the work, the time to collect these data, and the sophistication of the tools available to analyse and interpret them are considerable – in any case, more so that those involved in the aforementioned exclusion of kin selection.

Another interesting point is that the results of the study crucially hinge on a specific formal technique, which in turn involves a number of modelling choices, among which: the sets of plausible factors envisaged at the outset; the sets of parameters from which the artificial networks are generated (one set for each relevant factor[15]); the choice of the similarity metrics; and the criteria on which the actual network-artificial network fit is deemed good enough. This raises a number of familiar issues. Different choices may have led to different results. In addition, it is seldom accepted in the philosophical literature that simulation-based models can have a confirmatory power[16] – so it is difficult to say that the causal role of the four key factors in the manakin interaction structure has been confirmed.

Even more importantly for us, the results of the study do not directly confirm a reciprocity-based explanation of cooperation. Some

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[14] These measured the distributions of: edgewise shared partners, geodesic distance (minimal length between nodes) and degree (number of connections). See Edelman et al. (2014: 127-9) for details.

[15] For instance the decay parameters of the network links.

[16] Let us be clear that we are not implying that models can be confirmed. Theories or hypotheses can be (dis)confirmed, and models are tools that may bear on this confirmation process, for instance by suggesting empirical predictions for a given hypothesis.

factors may fit more direct reciprocity (e.g. link persistence) or indirect reciprocity (e.g. triad closure) scenarios. However, at best the results establish a number of possibly influential factors for the formation of interaction patterns (in kin selection, there would be only one such factor, genetic similarity). A full-fledged explanation of cooperative display among manakins would necessitate at least three more things. First, a description of the proximal mechanisms by which manakins actually associate with partners, that is, by which they select closer, higher-status, and/or long term partners. Second, a full explanation would necessitate a description of the evolutionary benefits and harms that are associated with the cooperative behaviours. Edelman et al's (2014) discuss possible benefits, although precisely those already mentioned by McDonald & Potts (1994). So some progress has been made, but not concerning the payoffs.

Finally, the issue regarding the multiple realisability of each explanation remains. Indeed, even if we assume that local processes of pattern formation have been identified, it remains to be seen whether they suffice to explain the precise behaviour of interest (here, cooperative display). Edelman and his coauthors note that similar processes have been found at work in the social behaviours of other animal species. For example, the four factors identified in manakin social structure formation are also important for the formation of human interactions,[17]; the two other factors, deemed non-explanatory in the manakin case, are also thought to be relevant to the human case. Do these latter two factors (to recall, selective mixing and preferential attachment) explain the considerable differences between manakin and human sociality? Does the interaction of these six factors lead to different behaviours in different species and/or distinct ecological contexts? Other local, yet unidentified properties may be explanatorily relevant. Relatedly, even if a reciprocity-based explanation turned out to be true in the manakin case, it may not be generalised to other cases, even if they involve the same relevant factors of pattern formation. In other words, hard work (extensive data collection, detailed observations, further model building) would be required again to confirm reciprocity-based explanation even in slightly different cases. This multiplies the amount of work needed for confirming reciprocity theory in general.

Combining our points in this section, and keeping the kin selection example in mind as a foil, we can see that Edelman et al.'s study involved a substantively higher quantity of work, the conclusion of

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[17] As evidence for this claim, Edelman et al. (2014) mention Capocci et al. (2006) on preferential attachment, Faust (2007) on triad closure, Goodreau et al. (2009) on triad closure and selective mixing, Preciado et al. (2012) on spatial proximity.

which is even weaker than the confirmation of a hypothesis. Moreover, we have no reason to think this would be any easier in a different case.

Now, what holds for confirmation holds for disconfirmation, with an extra kick. Imagine a tentative to disconfirm reciprocity-based explanations based on a pattern analysis such as above. Two scenarios are possible. Either one would have to examine with all possible predictive factors for pattern interaction, which means browsing an open-ended list; or if any does appear to have some predictive power, to examine all possibly associated payoff profiles, which are dautingly numerous as well[18]. In both cases, such work would be more demanding than the one just described, as it would require both more data and more analyses. Though feasible in principle, this is a daring task. Worrying anomalies will be hard to find indeed.

Overall, SET now appears to be closer to the adaptationist research programme than it first appeared. Despite its focus on specific, costly target traits and the small set of explanatory principles on which it relies, it leaves room for so many explanatory scenarios, and the (dis)confirmation of each is so demanding, that it is itself hardly amenable to (dis)confirmation as a whole. In other words, in the research programme–specific hypothesis interval, SET is closer to the former than we may have thought.[19] As a consequence, the puzzling cases emphasised in section 2 constitute scientific business as usual and should not be considered as threats but as opportunities for SET.

6. Explanatory scopes

So far, our argument regarding the difficulty of disconfirming social evolution theory can be summarised as follows:

> Premise 1: Social evolution theory is a set of various explanatory principles; so to disconfirm the latter, all of these principles should be disconfirmed.
> 2/ Premise 2: It is difficult to disconfirm one of SET's explanatory principles, namely reciprocity theory.
> 3/ Conclusion: SET is difficult to disconfirm.

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[18] This last scenario seems more plausible, as there will arguably often be at least a handful of factors with a moderate predictive power.

[19] We will see in section 7 why this does not make it a research programme either though, and that SET may received no such label as a whole.

From this conclusion, we then argued that SET appears closer to being a adaptationism-like research programme than to a theory – a set of specific hypotheses.

Although logically valid (and hopefully sound), the argument may be criticised because of the irrelevance of its conclusion. For who ever tries to confirm or disconfirm SET as a whole? What theorists are typically interested in is trying to (dis)confirm one particular explanatory principle among those that collectively constitute SET. And it may not matter much that reciprocity theories are difficult to disconfirm, especially if they have little explanatory scope and if other explanatory principles that have a wider scope are easier to disconfirm. In this section, we focus one one such candidate, namely kin selection, to counter such potential objections–and so to argue that we are not guilty of an undue focus on reciprocity theories.

First, how explanatory are reciprocity theories? It has long been though that their explanatory scope is limited, that is, that they may only explain a small subset of cooperative behaviours. This is because reciprocity is cognitively demanding, or at least more demanding than kin selection for instance. For direct reciprocity to be possible, individuals need to remember who they interact with and what the nature of these interactions was. For indirect reciprocity to be possible, individuals need to remember who interacted with other individuals either in a cooperative or non-cooperative manner. In order to identify potential cooperators or non-cooperators who you have never interacted with, you need to keep tabs on many individuals. If anything, reciprocity demands possibly heavy memory resources. As a result, it is thought to be rare among non-human animals, little of which possess this ability (Hammerstein 2003); and reciprocity theories would be automatically disconfirmed when this ability is absent.

Note, however, that such cognitive demands are not to be exaggerated. For instance, in an example of indirect reciprocity among song sparrows (Akçay et al. 2010), individuals become aggressive towards individuals they have never met when there has been a recent change of song in the neighbouring territory (indicating a recent change of ownership following the hostile intrusion of a non-cooperator). Here, indirect reciprocity may function without individuals keeping tabs on precise individuals; detecting changes in an otherwise fixed space structure, which is less cognitively demanding, is sufficient[20].

Even if reciprocity explanations have a slightly wider explanatory scope than previously thought, relevant cases remain uncommon. Con-

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[20] Regarding direct reciprocity, also note, as Okasha (2013 [2003] remarks, that it may also evolve in the absence of abilities for individual recognition "if each individual interacts with only one or a few other individuals throughout its lifetime".

trast it with explanations based on kin selection. One of their attractive features is that they are easier to disconfirm. For in order to exclude or at least lower the plausibility of a kin selection mechanism, one only needs to check the interaction structure: if cooperative partners do not involve an increased genetic similarity (as compared to the rest of the population), then kin selection cannot be at work. In particular, there is no need to go through the enormous list of possible cooperative benefits and costs. Positive assortment between parents is a necessary condition for kin selection to act; so the absence of such assortment suffices to eliminate kin selection from the list of possible explanations.[21] So if SET is difficult to disconfirm, this is not because of its kin selection component. As SET's kin selection component is closer to a set of hypotheses than to a research programme, SET itself may turn out to be more (dis)confirmable than we claimed, at least if a significant proportion of social behaviours turn out to be covered by kin selection.

So what about the explanatory scope of kin selection? Kin selection is typically seen as explaining a wide array of behaviours in domains ranging from sex allocation to parent-offspring or sibling conflict (Abbot et al. 2010). However, recent debates have cast doubt upon this impressive explanatory scope. We will mention two of them. First, one important, well-known consequence of kin selection regarding the evolution of altruistic behaviour is Hamilton's rule, namely the equation stating that such evolution will occur as soon as the individual fitness cost c is inferior to the fitness benefits b caused by a target individual for others, weighted by their relatedness r (Hamilton 1964, Birch 2017)–in short, when $rb > c$. But this rule can be expressed in two different ways. As it is described above, it is explanatory but almost never true: the inequality only guarantees the evolution of an altruistic behaviour under a number of very restrictive simplifying assumptions. Now, one may also express a generalised version $RB > C$, which this time guarantees such evolution. However, the coefficient B, C and R are now purely statistical quantities, which can no longer receive a straightforward causal interpretation (Gardner et al. 2011, Birch & Okasha 2014). In other words, one core component of kin selection is either explanatory and almost always false, or always true while having weak explanatory power. The explanatory scope of kin selection thus receives a serious blow.[22]

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[21] Of course, in order to confirm a kin selection explanation, one would have both to check the interaction structure and to assess the fitness benefits and costs involved; for a classic example of such a study, see Mumme 1992.

[22] Note that this point does not hinges on the nature regarding the links between kin and group selection, which as been the topic of other recent discussions. These typically concern the comparison of the explanatory scopes of kin and group se-

A second reason to reassess the explanatory scope of kin selection is that it is no longer clear whether it includes its seminal case, namely worker sterility in haplodoploid eusocial groups. According to the traditional analysis, the reason why workers do not lay eggs but care for their queen's is that their are more closely related to their sisters than to their own progeny (their relatedness being 0.75 and 0.5, respectively). However, relatedness coefficients as high as 0.75 are seldom observed in eusocial colonies, either because of multiple queens or of multiple mating partners (Bourke & Franks 1995). One possibility is thus that kin selection may not be a crucial process for the appearance and stability of eusocial colonies but a secondary one, whose efficiency would be both preceded and favoured by group selection (Wilson & Hölldobler 2005). As colonies tighten up, kin structure may then tend to disappear entirely (van der Hammen et al. 2002).

Here is not the place to assess these claims. However, they suffice to show that attributing a wide explanatory scope of kin selection is debatable for both conceptual and empirical reasons. Consequently, it would be premature to reject doubts regarding reciprocity theories by arguing that they constitute but a negligible part of SET. In other words, while the absolute domain of application of reciprocity theories is limited (to organisms that possess the required cognitive abilities or exist in specific conditions), their relative domain within SET isn't negligible.

Two final notes. First, the foregoing does not entail that kin selection may not enjoy some kind of priority over reciprocity theories. When a behaviour belongs to a type of phenomena thought to fall within the purview of both theories[23], kin selection will probably be tested first. This is not, however, because it is deemed more explanatory, but because it is easier to disconfirm. Second, again because kin selection explanations are easier to disconfirm than alternative (e.g. reciprocity-based) ones, the relative explanatory scope of such alternatives is likely to be overestimated, and thus that of kin selection underestimated. Still, in general intuitions regarding explanatory scope will be too tentative to draw a priori conclusions regarding the relevance of such or such principle within SET. The confirmatory difficulties that affect reciprocity theories thus concern SET as a whole.

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lection, and whether one logically entails the other. But even if some kin selection processes ended up being labelled as cases of group selection, the question of the relative scope of reciprocity theories would remain unaffected.

[23] That is, when it concerns species in which reciprocal altruism is possible to begin with.

7. What is social evolution theory?

We are now in a position to assess the nature of social evolution theory. Is it a theory or a research programme? The foregoing reveals that it is neither.

First, despite its name, social evolution theory is not a theory. A theory is usually taken to consist in, or involve a set of hypotheses. Intuitively, one may thus think that SET fits this description, as it is based on multiple explanatory principles, each of which may lead to the formulation of more specific hypotheses in specific cases of social behaviour. However, the various hypotheses that compose a theory are in general compatible : they can be and often must be combined in order to explain or predict observations (consider for instance Newton's laws of motion and his law of gravitation). By contrast, SET's different explanatory principles generate alternative, competing hypotheses that aim to explain on their own. In other words, the typical question to be investigated in SET is whether a given social behaviour is better explained by kin selection, by reciprocity mechanisms, etc. The debates concerning the respective explanatory scope of various principles, discussed in the previous section, bring out this competitive, rather than complementary, relationship between the principles.[24] As a result, if SET is a theory, it is an uncommon one.

One may thus think that SET is rather a research programme, which appears to be an orthodox view.[25] However, this is far from straightforward. According to Lakatos' (1970) famous account, a research programme involves both core and auxiliary hypotheses. The former are stable and steer the formulation of observable consequences, while the latter can be reformulated and abandoned depending on how they fare empirically. If we were to say that SET is a research programme, its auxiliary hypotheses may be whatever specific hypotheses are derived from any of its core principles. For instance, within kin selection, an auxiliary hypothesis may be that interaction between relatives stems from kin recognition, or from population viscosity (recall section 4.2). Insofar as the basic mechanisms are multiply realisable, any auxiliary hypothesis may be equated with a suitable class of similar realisations.

What could be a core hypothesis of SET though? As we saw in section 6, several candidates have been offered, such as the generalised version of Hamilton's rule (Gardner et al. 2011, Birch 2017) or the

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[24] This does not mean that the principles may not be combined: a social behaviour may well result from the combined action of kin selection and of a reciprocity mechanism. This, however, is seldom the default scenario.

[25] For instance, according to Birch, “Hamiltons pioneering work kickstarted a research program now known as social evolution theory” (2018: 4).

principle of positive assortment (Fletcher & Doebeli 2009). Another possible candidate may be the Price equation itself, from which the generalised version of Hamilton's rule can be derived (Lehtonen 2020). However, although it may be argued that such candidates provide a unificatory framework for SET, they must be distinguished from a core hypothesis. Core hypotheses are supposed to be of heuristic use and to ultimately lead to the formulation of predictions (in the sense of observable consequences). Core hypotheses are what allows for a progressive research programme, which keeps generating empirical hypotheses.

By contrast, the three possible principles just mentioned have hardly been instrumental in the empirical success of SET. Rather, they have been put forward *a posteriori*, and in particular after the main explanatory principles that compose SET have been identified. Positive assortment, the generalised Hamilton's rule, the Price equation stem from attempts to unify a scientific entity, namely SET, that had been lacking such unification so far.

Couldn't SET's conceptual core be the principle natural selection itself? Not quite. First, this would make SET nothing more than adaptationism applied to the domain of social behaviours, which would be strange given the limited number of explanatory principles on which it relies (see section 2). Second and more importantly, SET may include partly non-selective explanations, as noted by Birch (2018: 61). It may for instance involve drift, as is the case in computer simulation-based analyses of the evolution of cooperative strategies. The relation between SET and adaptationism is thus one of partial overlap.

In fact, when asked to identify principles that have led to the formulation of empirical consequences in SET, theoretical biologists tend to mention one of its explanatory principles–most often kin selection. For instance, according to Gardner & West (2014):

> Clearly, inclusive fitness is not a single hypothesis, but rather represents an entire programme of research. Scientific hypotheses are judged according to how amenable they are for empirical testing and how well they resist attempts at empirical falsification. By contrast, scientific research programmes are judged according to how well they facilitate the formulation and testing of hypotheses – that is, stimulating the interplay between theory and empiricism that drives progress in scientific understanding. For example, inclusive fitness theory has yielded a number of hypotheses concerning the factors driving the evolution of insect eusociality [...]

This comment suggests that the 'research programme' label may fit those parts of SET in which core principles play their driving role. However, this does not entail that the label can be usefully applied to SET itself.

What is the upshot of this discussion? Overall, our final description of SET is as follows. SET is captured neither by the 'theory' label nor by the 'research programme' one. Rather, it is a set of various parts. Some of these parts may be research programmes (e.g. kin selection theory), leading to hypotheses that are at least partly amenable to (dis)confirmation. Other parts, such as reciprocity theory, lead to hypotheses that more impervious to (dis)confirmation. From the confirmatory perspective, SET is a heterogeneous scientific entity– a *confirmatory patchwork*.[26] It is mostly characterised by its domain – the set of behaviours it targets – than by a conceptual core or by a shared aspect of its components.

8. Conclusion

How should we assess the consequences of cases of unexplained cooperative behaviours for social evolution theory, which is supposed to make sense of them? Our conclusion is that such cases pose no direct threat. At first glance, social evolution theory may appear as a set of testable, specific hypotheses, which are open to (dis)confirmation. This is because it targets only a specific set of traits and is based on a handful of explanatory principles.

However, social evolution theory turns out to be quite impervious to (dis)confirmation. More precisely, while some of its components (e.g. kin selection) may be easy to (dis)confirm at least, others (e.g. reciprocity theories) are as impervious to (dis)confirmation as adaptationism itself is, because of their compatibility with an unrestricted list of evolutionary scenarios.[27] As a result, social evolution theory is a confirmatory patchwork, whose components fare differently, confirmation-wise. In the face of yet unexplained cases of cooperative behaviours, social evolution theory displays no sign of illness.

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[26] Interestingly, while he considers SET as a research programme, Birch also describes it as a heterogeneous set, although with respect to the variety of its modelling approaches (2018: 47).

[27] Incidentally, it is striking that a proper, restricted part of adaptationism retains its confirmatory characteristics.

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