# GENETIC RELATEDNESS AND ITS CAUSAL ROLE IN THE EVOLUTION OF EUSOCIALITY

**Tuomas K. Pernu**
**King's College London**
**&**
**Heikki Helanterä**
**University of Oulu**

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**Abstract.** The role of genetic relatedness in social evolution has recently come under critical attention. These arguments are here critically analyzed, both theoretically and empirically. It is argued that when the conceptual structure of the theory of natural selection is carefully taken into account, genetic relatedness can be seen to play an indispensable role in the evolution of eusociality. Although reviewing the empirical evidence concerning the evolution of eusociality reveals that relatedness does not play a role in the initial appearance of eusociality, this follows simply from the fact that natural selection – of which relatedness is a necessary component – does not play a causal role in the origin of any traits. Further, separating two logically distinct elements of causal explanation – necessity and sufficiency – explains why the debate lingers on: although relatedness plays a necessary role in the evolution of eusociality, relatedness alone is not sufficient for its appearance. Therefore, if the relatedness variable in a given data set is held at a uniformly high value, then it may indeed turn out that other factors become to occupy a more salient role. However, this does not change the fact that high relatedness functions as a necessary condition for the evolution of eusociality.

**Keywords.** behavioral ecology; causal explanation; causal necessity; causal sufficiency; causation; group selection; inclusive fitness; kin selection; levels of selection; models; natural selection; necessary conditions; sociobiology

## 1. Introduction

The role of genetic relatedness in social evolution, especially in the evolution of eusociality in insects, has recently become under critical attention (Allen *& al.* 2013; Nowak & Allen 2015; Nowak *& al.* 2010; Wilson 2008; Wilson & Hölldobler 2005; Wilson & Nowak 2014; Wilson & Wilson 2007). This argumentation has also been extensively criticized (*e.g.* Abbott *& al.* 2010;

Boomsma *& al.* 2010, Liao *& al.* 2015). Much of the criticism and ensuing discussion has revolved around the relative merits of different modeling approaches (Rousset & Lion 2011; Birch 2014; Birch & Okasha 2014), semantic issues surrounding co-operation and altruism (West *& al.* 2007), and most recently, the interpretation of different formulations of inclusive fitness approaches and their causal implications (Allen *& al.* 2013; Birch 2014; Birch & Okasha 2014).

However, one central claim of the argumentation merits further critical attention. This is the claim that the genetic relatedness of eusocial organisms has played no causal role in the evolution of eusociality. Here is a representative series of quotes illustrating this line of argumentation:

> “[T]he known background biology of the eusocial insects, in particular the hymenopterans, gives no reason to presuppose that pedigree kinship is a key causative element in the origin and early evolution of eusociality.” (Wilson 2008, p. 22.)

> “[W]hile close pedigree kinship among group members inevitably accompanies the origin and early evolution of eusociality, the association is a by-product of preadaptation and not a causative condition.” (Wilson 2008, p. 22.)

> “Two conditions working together, key preadaptations and strong proportionate group selection, are from the evidence necessary and sufficient for eusociality. Close genetic relatedness and collateral kin selection are not necessary.” (Wilson 2008, p. 22.)

> “[R]elatedness is better explained as the consequence rather than the cause of eusociality.” (Nowak *& al.* 2010, p. 1060.)[1]

> “Grouping by family can hasten the spread of eusocial alleles, but it is not a causative agent.” (Nowak *& al.* 2010, p. 1060.)

> “While similarity of genomes by kinship was an inevitable consequence of group formation, kin selection was not the cause. The extreme limitations of kin selection and the

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[1] This claim, almost in verbatim, is also made by Wilson & Hölldobler (2005, p. 13367) and Wilson & Wilson (2007, p. 340).

> phantom-like properties of inclusive fitness apply equally to humans and to eusocial insects and other animals.” (Wilson 2014, p. 74.)

> “Does ’relatedness’ cause evolution of eusociality?” (Nowak & Allen 2015, p. 3/5.)

These statements are regrettably vague, even in their original contexts. We think, however, that by voicing them the critics intend to make novel and substantial claims about the evolution of eusociality, and that statements like these form the conceptual kernel of their argumentation. It is generally agreed, as will be explained in more detail below, that relatedness between reproducing individuals and their helpers has been high when eusociality has first evolved. But it has been wrong to think, the critics seem to suggest, that this would imply that genetic relatedness is a causal factor in the evolution of eusociality. Is this really so? Has the received view in fact assumed that genetic relatedness is such a factor? And, if it has, has it made a mistake in doing so? What, in the first place, does it mean to claim that relatedness is, or is not, a causal factor in the evolution of eusociality? It seems that these are the central questions to address in order for the discussion to make progress.

We aim to clear this issue – or at least some of it – by relating the issue of relatedness and the evolution of eusociality to a more encompassing conceptual view on the theory of evolution. We think that the key to taking steps towards resolving the issue lies in the intersection of conceptual analysis and empirical biology: we intend to not get lost in the details of neither approach – which we think is a drawback of many of the previous takes on the issue (both pro and con) – but instead present a general analysis and provide a framework with both conceptual and empirical dimensions to help us to assess the claims about the causal role of relatedness in the evolution of eusociality.

Our discussion proceeds in three steps. First; we examine in detail the role of relatedness in the evolution of eusociality in the light of a widely accepted general formulation of the theory of evolution by natural selection. We argue that there are purely conceptual reasons to think that genetic relatedness must feature as a necessary component in the evolution of eusociality. Whether this component is interpreted causally, however, depends on the general stance one takes on the causal role of natural selection in evolution.

Second; we present a widely accepted and empirically backed up scenario for the evolution of eusociality and examine the role of genetic relatedness in it. It is noted that although it is true that relatedness does not play a role in the initial appearance of eusociality, this follows simply from the fact that natural selection – of which relatedness is a necessary component – does not play a causal role in the origin of *any* traits. Hence, on a closer analysis disavowing the causal role of relatedness in the evolution of eusociality is either trivially false or trivially true: on the one hand, as a necessary component of natural selection, genetic relatedness must play an indispensable role in the evolution of eusociality; on the other hand, genetic relatedness – due to its very role as a necessary component of natural selection – cannot play a role in the initial appearance of eusociality. These results follow simply from the conceptual structure of the theory of natural selection.

Third; we analyse causal claims to consist in two logically distinct components: the *necessity element* and the *sufficiency element* (*cf.* Mackie 1965, 1974). When we say that *X* causes *Y*, we often equivocate between two distinct claims: that removing *X* will result in removing in *Y* (necessity), and that producing *X* will produce *Y* (sufficiency). Keeping this distinction in mind will turn out to be particularly useful in this context. Although genetic relatedness can be show to be a necessary condition for the evolution of eusociality, it clearly is not sufficient. This explains why some of the critical claims can be interpreted to be true. However, many of them can now also be shown to be unequivocally false.

Let us make a few terminological clarifications before moving on. Although we think that the lessons of this discussion are relevant to the topic of evolution of social behavior in general, we confine our discussion to eusocial behavior of hymenopterans because its evolutionary history is most clearly articulated in the currently existing literature. *Eusociality* is a population level notion: it refers to reproductive division of labor among separate individual organisms, queens and workers. *Altruism* is a more general notion that refers to a type of behavior displayed by an individual organism, namely behavior that benefits other organism(s) at the cost of the altruistic organism. It is clear that there is a wide range of social behavior in the animal kingdom (*e.g.* cooperation, reciprocity, mutualism, synergism) that differs from the genuinely altruistic, eusocial behavior because they accrue direct benefits to the cooperating individuals (West *& al.* 2007). Whether these sorts of behavior are *really* altruistic or not is not of concern right now. By *eusocial altruism* we mean eusocial behavior where an organism with a sterile phenotype is confined to helping other organism(s) (eusocial egoists) to reproduce.

## 2. Relatedness and natural selection

Let us start from a common ground. Although the issue is not explicitly addressed, it is clear that all parties in the debate presuppose that eusociality is an adaptation. That is, eusocial behavior has evolved by means of natural selection. In other words, eusociality is not a "spandrel" (*sensu* Gould & Lewontin 1979).

There should also be no disagreement with respect to what evolution by natural selection fundamentally amounts to. Let us start with a textbook definition of natural selection: natural selection is "*any consistent difference in fitness among phenotypically different classes of biological entities*" (Futuyma 2005, p. 251). Fitness, in turn, is the average number of offspring, or realized reproductive value of any given type of biological entity. Fitness values can be attributed to particular types of organisms as their mean reproductive success. And an individual organism of this type has a certain probability of producing a given amount of offspring, or an expected fitness value.

What should also be clear is that natural selection may well operate in the absence of evolution. This is again a basic truism, but one that touches the core of the current debate. Suppose we have variation in fitness in certain types of biological entities. What this means is that certain types of entities – organisms with a particular trait – are reproductively more successful than some other types of entities. What this does not mean, however, is that the first type of entities would increase their relative number in the given population. Why? Simply because it was not assumed that the offspring would be of the same type as their parents. *I.e.*, it was not assumed that the trait in question is *heritable*.

What we are arriving at are the three basic components of evolution by natural selection. A population *P* is evolving by natural selection with respect to a trait *T if, and only if*:

1. There is variation in *P* with respect to *T*.
2. Variation in *T* is associated with variation in fitness in *P*.
3. Variation in *T* is heritable in *P*.

For evolution by natural selection to occur, all of these are necessary and none of them alone is sufficient. This is one of the most fundamental ideas of evolutionary theory, and as such, should not be under dispute. Since those doubting the causal role of relatedness in the evolution of eusociality have explicitly stressed that they base their arguments primarily on population genetics (*e.g*. Nowak *& al.* 2011), we take it that they must be subscribing to this basic idea as well.

But now problems arise. By simply substituting "eusociality" for *T* we get the following. In order for eusociality to have evolved by natural selection there must have been variation with respect to eusociality, this variation must have had fitness consequences – eusocial organisms must have reproductively more successful than other types of organism – and eusociality must have been heritable. Once these elements are in place, eusocial behavior will become prevalent (in the given population). But all of these are needed; none of them is superfluous. In particular: eusocial organisms must have been breeding eusocial offspring. Otherwise the trait would not have spread.

As already stated, the defining feature of eusociality is the reproductive division of labour where only a few organisms reproduce at the help of sterile altruists. So the question springs up: how could evolution by natural selection have brought about and maintained such altruism? If organisms with a trait *T* do not produce offspring bearing the same trait, then it is clear that such a trait cannot become prevalent by means of natural selection. Since eusocial altruists are not reproducing, it seems conceptually impossible that such a behavior would have been evolved by natural selection.

Such a conclusion would go against the original assumption: it has been taken for granted, by all parties, that eusociality is an adaptation. The only way how that assumption could be true, it now seems, is that the behavior is heritable by a route other than direct reproduction. But how could that happen? Here is where the ways part. The conventional reply would invoke the notion of inclusive fitness (and relatedness as a key component of inclusive fitness): although the eusocial altruists are not reproducing themselves, by helping their close relatives to breed they are indirectly passing on their own genes to the next generation. Since there is a high probability that the close relatives that are receiving the help of the altruists share the same genes as the altruists, the altruistic behavior passes on to the next generation through the offspring of the close relatives. In this way the seemingly maladaptive behavior can evolve and be maintained by natural selection.

But the critics now deny this explanation. According to them close genetic relatedness has not played a causal role in the evolution of eusociality (*cf.* the quotes above). Instead of invoking inclusive fitness it is claimed that individual selection on the genotype of the queen, and later as more advanced eusociality appears, selection on the level of nests, is all that is needed for eusocial behavior to evolve. What the critics do not deny is that we can now observe high degree of relatedness among group members in eusocial populations. That is again something that is not under dispute. It's just that according to the critics this high degree of relatedness that we now observe is a consequence rather than a cause of the evolution of eusociality. This, however, seems very baffling in the light of what the theory of natural selection amounts to.

Now, to be clear, the statements made by the critics seem to lend themselves to a variety of interpretations. First, one could interpret them in light of a more general claim according to which natural selection is not a causal factor in evolution. Hence relatedness would fail to be causally related to the evolution of eusociality simply because natural selection fails to be causally related to the evolution of any traits (and relatedness is a necessary part of natural selection). We think that this claim is in fact in the heart of the matter and we will discuss it below (this section). Second, one could try to interpret the statements to amount to granting a causal role to natural selection but holding on to an idea that heritability – and hence relatedness – is not a causal component in natural selection. However, it is difficult to make sense of this claim: heritability is a necessary element of evolution by natural selection, not something that is additional or supplementary to it, and hence granting a causal role to natural selection while denying such a role from one of its legs does not seem amount to a coherent position. Third, one could interpret the statements to claim that even though both natural selection and heritability as its necessary component are causal factors in the evolution of eusociality, it is wrong to think that relatedness is necessary for heritability. We take this to be an interesting and substantial claim, but lacking adequate empirical backing. Fourth, one could take the statements to claim that relatedness is insufficient for eusociality to evolve (Liao *& al.* 2015). Given that there are numerous organisms that live in high relatedness groups but are not eusocial, relatedness is clearly not sufficient for eusociality to evolve, but other biological factors must also play a role. But this should not come as news to anybody, since ecological factors have been essential parts of social evolution theory since Hamilton's seminal papers (Hamilton 1964). Moreover, noting that relatedness is not *sufficient* for eusociality to evolve only highlights the fact that it seems to be *necessary*, and that is the idea that the critics should be attacking. Nevertheless, understanding that appealing to necessity and sufficiency constitute distinct causal claims holds the key to unraveling the debate, as it will be shown below (section 4).

Supposing that these interpretations exhaust all the available options, there seems to be two significant claims to address. The first concerns the conceptual issue of the causal status of natural selection in evolution. The second concerns the empirical issue of genetic relatedness as a component of heritability. Supposing that heritability of a trait is a necessary part of *any* evolutionary explanation that invokes the notion of natural selection the critics owe us an account of how eusociality is heritable without close intracolonial relatedness. Heritability and genetic relatedness are not synonymous, of course. So in principle one could accept all the three fundamental conditions of evolution by natural selection, but deny that genetic relatedness plays a role in the evolution of eusociality. But that would mean that the necessary correlation between parent and offspring would have to rise through non-genetic means. We discuss in the next section why such an "extended inheritance" scenario is unlikely (section 3.3b). In the remainder of this section we will highlight the theoretically problematic issues the critics of the conventional explanation are facing.

The fundamental conceptual question is this: if a trait must be heritable in order for it to have been evolved by means of natural selection, is there any sense in claiming – or denying – that the heritability of the trait is *causing* its evolution? We think not. Such claims involve a conceptual misunderstanding about the structure of the theory of evolution.

The fundamental conditions of evolution by natural selection are definitional elements of the notion. Evolution by natural selection is not something that follows logically from the conditions or something that is caused by them. Rather, evolution by natural selection *is* those conditions. Whenever all the three conditions hold, evolution by natural selection is in operation, but not as something that comes after, or over and above the three conditions it is composed out of. Hence heritability, being one of those conditions, is never causing the evolution of any traits, not because it has no role in evolution, but because its function in the process is wholly conceptual.

What also follows from this, we think, is that evolution by natural selection is a wholly statistical process. Given a population where the fundamental conditions of evolution by natural selection hold, the population evolves by necessity (barring mutation, drift and migration). Neither the components of evolution by natural selection nor natural selection itself are causes of this evolution. Evolution by natural selection is simply a statistical process that the given population undergoes when the fundamental conditions happen to hold.

Although all this seems to follow from the notion of natural selection rather trivially, we acknowledge that it may come to clash with some well-established intuitions with respect to evolution by natural selection – namely the idea that it is exactly natural selection that is the primary cause, mechanism, or force of evolution (*cf*. Futuyma 2005; Mayr 1982; Sober 1984). If evolution by natural selection is a process by which evolution happens, then, strictly speaking, it does not seem to function as its cause. Whether natural selection is a cause of evolution has recently been heavily debated (*e.g*. Reisman & Forber 2005; Walsh *& al.* 2002). We will not indulge in this debate here. We only note that although there might be a sense in which natural selection and evolution are causally related, the fundamental statistical nature of evolutionary theory should not be questioned.

There is also another debate that relates directly to the issue at hand. This is the debate about the positive *vs* negative role of natural selection in evolution. Although it might seem appealing to think that natural selection gives an explanation for the phenotypic traits of organisms (Neander 1995), its role should actually be seen wholly negatively (Cummins 1975; Dretske 1990; Sober 1984; Sober 1995). That is, natural selection does not act by creating adaptive traits, but only by eliminating those that are not adaptive. This is again something that seems to follow directly from the fundamentally statistical nature of evolutionary theory. But then it is again rather obvious that relatedness does not play a causal role in the evolution of eusociality; natural selection is simply not contributing positively to the origin of *any* traits.

So there are at least two conceptual issues that those in doubt of the causal role of relatedness in the evolution of eusociality must face. First, heritability – and in this context genetic relatedness – is a necessary condition of evolution by natural selection. As such, genetic relatedness has to play an indispensable role in the evolution of eusociality. Second, given the fundamentally statistical nature of the theory of evolution, it does not seem to make sense to talk about the causal role of heritability or natural selection. Hence denying the causal role of relatedness in the evolution of eusociality does not seem to amount to a substantial claim.

## 3. Evolutionary scenario for eusociality

In the following we review the role of relatedness, and the question whether it can be interpreted in causal terms, at the key stages of evolution of eusociality. We present an evolutionary scenario for eusociality from a solitary ancestor to a species with advanced eusociality with morphologically separated queen and worker castes, where workers have lost the option of independent reproduction. This scenario is similar to the ones recently proposed by Nowak *& al.* (2010) and Hunt (2011). It is widely agreed that the ancestors of eusocial hymenopterans were solitary wasps and bees with a nest and maternal care of offspring. We concentrate below on the so called "life insurer" -route to eusociality, thought to apply to the social hymenoptera (in contrast to the "fortress defender" -route of termites, aphids and thrips (Queller & Strassmann 1998; Ross *& al.* 2013)). Furthermore, we concentrate on the subsocial route to eusociality (*i.e.* associations of mothers and helper daughters), since the alternative parasocial or semisocial route (where the same generation females associate to breed cooperatively) has in the light of empirical evidence never lead to eusocial species (Bourke 2011).

To facilitate the dissecting of the role of relatedness in evolution of eusociality, we have split the evolutionary scenario into four stages (closely following Hunt (2011), Nowak *& al.* (2010) and Wilson & Nowak (2014)). Our aim is to make it clear that even if relatedness does not play a role in all the steps, and is clearly not alone sufficient for the evolution of eusociality, it plays an indispensable role at a crucial stage, and is thus a necessary condition for the evolution of eusociality.

### *1. Group formation and preadaptations*

As a first stage in the evolution of eusociality we need to consider a suite of traits present in the ancestral state before the helper phenotype arises. These include a defensible nest, overlapping generations, parental care by the mother, and the presence of siblings in need of help when offspring emerge. Phylogenetic reconstructions also suggest that the ancestors of each independent origin of eusocial hymenoptera had monogamous mothers, which guarantees high relatedness within the group (Boomsma *& al.* (2010) and references therein). It is clear that relatedness plays no causal role in the emergence of these preadaptive traits. However, relatedness is an inseparable part of the family structure of the mother-offspring associations.

The preadaptations can be ordered on a scale of salience with respect to eusociality (Hunt 1999, 2011). Single mating that guarantees high relatedness to siblings for the helpers has been argued to be a trait of low salience, since it may well have been shared by many lineages that did not evolve sociality (Hunt 2011; Nowak *& al.* 2010). However, low salience, and the possible lack of statistical association between eusociality and ancestral monogamy, and the fact that high relatedness *per se* has not been the reason why monogamy occurs in these taxa (monogamy can be selected for due to *e.g.* costs of mating, as outlined in Wilson & Nowak (2014)) does not change the necessary role of relatedness in subsequent stages of the evolution of eusociality, as outlined below.

### *2. Emergence of a facultative helper phenotype; eusociality threshold*

A scenario for the emergence of a facultative helper phenotype that seems likely in the face of current genetic evidence (Hunt & Amdam 2007, Toth *& al.* 2007) is the co-option of maternal care behavior to allomaternal care, through *e.g.* modifications of dispersal and diapause behaviors (Hunt 2011). This fits the view that eusocial worker phenotypes are facultatively expressed with no fixed genetic differences among castes (an allele for obligate altruism would not spread in the population; Queller & Strassmann 1998). This seems to be the case throughout social hymenopterans apart from a few exceptions found in highly derived lineages (Schwander *& al.* 2010).

It is clear that relatedness does not play a causal role in the emergence of the helper phenotypes, and is not a phenotypic trait of individuals or groups interacting with the environment, and causing differences in reproductive success. However, this is just a trivial consequence of evolutionary theory. Evolution by natural selection, and relatedness as its part, does not play a causal role in the origin of *any* phenotypic traits. According to the received view (of the modern synthesis) new traits are produced through mutation or recombination. Relatedness is not causally linked to these phenomena. Whether the received view is fully able to account for the appearance of evolutionary novelties is not of concern right now (*cf.* Pigliucci &

Müller 2010). It may be that relying on mere mutation and recombination is a too pruned view of the evolution of novelties. However, what is missing from the picture, if anything, is the ontogenetic point of view. Relatedness clearly is not a part of developmental processes either. Thus, it can be safely assumed that even if an "extended synthesis" is called for to account for evolutionary novelties, relatedness does not come to play a causal role in the initial appearance of eusociality.

### *3. Spread of the helper phenotype in the population; entrenchment of the helper phenotype in development*

In the next step we consider two simultaneously occurring processes. The helper phenotype has to spread in the population, and its development has to be made robust, "entrenched" or "canalised" (West-Eberhard 2003). For both of these processes we have to consider two crucial things in the evolutionary process: the selective benefit, or the fitness effect, of a trait on the one hand (a), and its inheritance on the other (b).

*(a) Selective benefit.* The helper individuals may have accrued direct fitness benefits in the early stages of eusocial evolution, *e.g.* laying some of their own eggs, or by later inheriting the nest and the position as the queen. However, now it is only relevant to consider the fitness effects of investing into the individually costly helping trait, since that is the eusocially altruistic trait that we are aiming to explain (as opposed to fundamentally mutualistic or reciprocal traits). The likely routes to the benefits of helping, and the ecological scenarios under which they should be relevant, have been considered at length elsewhere (Gadagkar 1990; Queller 1989, 1994). The key feature of these scenarios is the indirect fitness benefit that the helper gains from helping her mother. Here the role of relatedness can be seen as determining the optimal behavior of the helper in terms of inclusive fitness: helping is not selected for unless relatedness between the helper and the helped is large enough to compensate for the direct fitness losses of the helper (Hamilton 1964). Monogamy of the mother guarantees maximum relatedness between the helper and the helped. Moreover, Liao *& al.* (2015) have demonstrated the necessary role of high relatedness by varying the relatedness variable in the models presented by Nowak *& al.* (2010) (which they claimed to show that relatedness is not an important factor in the evolution of eusociality). However, as the above discussion has tried to make it clear it does not make much sense to couch this relationship in causal terms.

*(b) Inheritance.* As already emphasized, the necessary role of relatedness becomes clear when the focus shifts to heredity of traits. Unless a given trait is heritable, it will not spread through natural selection. In this particular case this means that unless the helper and the helped are relatives, the helper trait does not spread even if the trait of the helper increases the reproductive success of the breeding individual (for otherwise the reproductive individual has merely a random chance to pass the gene to the next generation).

This simple genetic inheritance scenario gets more complicated if the trait is not based on simple genetic inheritance at the individual level. Under an extended view of heredity (Danchin *& al.* 2011; Helanterä & Uller 2010), the helper phenotype that in the standard view is based on the plastic expression of the genes carried by both the reproducer and the helper, can for example be induced by an environmental (abiotic, biotic or social) feature, be inherited epigenetically, or be based on coercion by the reproducer even in the absence of genetic similarity. Whether helping behavior is determined by maternal or helper genes affects the conditions under which helping behavior is selected for (Liao *& al.* 2015), so that under maternal control even unrelated helpers may be favored by selection, which we treat here as a group level heritability brought about by coercion. Effectively, these mechanisms can be seen as creating heritability at the level of the group phenotype and the division of labor into reproducer and helper. In other words, any mechanism that ensures the presence of a helper in the new group founded by a dispersing reproductive female, even if the plastic helping phenotype is not coded in the genome of the foundress, is enough to ensure high heritability of the group phenotype. Group heritability is a difficult and underexplored issue (Okasha 2006), and even group selection treatments of social evolution may rely on heritability that is causally attributed to the individual level (Marshall 2015, p. 92). More importantly for the current discussion, there are empirical reasons why the non-genetic mechanisms that could cause group heritability are unlikely to underlie the evolution of sophisticated eusocial adaptations. This is because at the early stages of facultative eusociality the helpers have independent reproductive options available (Hunt 2011). If the helping behavior is induced non-genetically and is not directed at relatives, or is not beneficial enough, then at the level of the helper genome selection should favor genetically inherited traits that either enhance competition for reproductive position or increase the chances of opting for solitary reproduction and abandoning the group. This would result in intra-organismal conflict over the helping trait and consequently helping behavior should be an evolutionarily transient phenomenon, and not further the evolution of eusociality. Similar logic applies in scenario where eusociality is based on green beard co-operation (Bourke 2011; Helanterä & Bargum 2007; Queller 2011) – selection for efficient helping that results in the evolution of advanced eusociality is likely only when all of the helper genome (or its extended inheritance equivalent) has a shared interest in helping.

### *4. Irreversibility threshold; advanced eusociality and its elaboration*

The further the eusocial evolution proceeds, the less beneficial are the independent reproductive options available for the helpers compared to the indirect fitness benefits of helping. This change in the benefit/cost ratio relaxes the requirement for constantly high relatedness within groups. In advanced eusocial organisms the workers have given up their independent options already during their development into adults. At this point the control of caste fate is largely in the hands of the individuals that rear the brood (Ratnieks & Helanterä 2009) who maximize their inclusive fitness through efficient colony functioning. Eusociality has evolved into a stage where it is difficult to imagine a reversal to a solitary breeding strategy. Loss of worker castes has secondarily occurred in socially parasitic "inquiline" ants, but they are highly specialized exploiters of worker force of other social insects (Buschinger 2009).

However, even after this irreversibility threshold has been reached, relatedness continues to play a role in guiding the evolution of elaborations of eusociality. While empirical evidence suggests that relatedness is not consistently high in advanced eusocial species, and even that low relatedness may be beneficial in some circumstances (Van Zweden *& al.* (2012) and references therein), relatedness continues to play a necessary role in social evolution. Relatedness among group members plays a crucial role in how genes expressed only in workers, or genes with indirect phenotypic effects, respond to selection (Bijma 2011; Linksvayer & Wade 2009; McGlothlin *& al.* 2010), and plays a necessary part in elaboration of social traits even when selection can effectively be seen as functioning at the group level, and societies approach "superorganismality" (Boomsma & Gawne 2017; Bourke 2011; Gardner & Grafen 2009; Helanterä 2016). Furthermore, relatedness plays a role in affecting optimal allocation decisions in conflict contexts, such as sex and caste allocation, and the amount of worker reproduction (Ratnieks *& al.* 2006), and thus contributes to the stability of the societies – it seems possible that societies where relatedness is very low are evolutionary dead ends (Helanterä *& al.* 2009; Queller & Strassmann 1998).

## 4. Necessity, sufficiency, and causal claims in evolutionary context

Reality is multifactorial. The biological realm in particular, as it is widely acknowledged, is notoriously complicated. Different pathways can typically lead to one and the same outcome, and we can always point to multiple factors that have a relevant role to play in the particular result we happen to be interested in. And which of these factors we choose to pinpoint as "causes" depends often crucially on the more general framing of the issue at hand.

The preceding analysis has revealed that there are both conceptual and empirical reasons to conclude that relatedness functions as a necessary condition for the evolution of eusociality. Should this now lead one to claim that relatedness causes the evolution of eusociality? Or should one perhaps draw the opposite conclusion? In abstract, both of these conclusions can actually be argued to have support. The reason for this is simply that necessary conditions can sometimes be deemed causes, other times not, depending on how the issue has been framed. And this ambivalence, it now becomes apparent, is the source of the current disagreements on the role of pedigree relatedness in the evolution of eusociality; the question "[d]oes 'relatedness' cause evolution of eusociality?" (Nowak & Allen 2015, p. 3/5) is in fact equivocal.

To illustrate this, consider figures 1 and 2 [figure captions at the end]. Figure 1 represents a hypothetical example of relatedness and social behaviour as continuous variables. The figure shows two ways of delineating the data. The smaller, red area covers cases where both relatedness and sociality are high. Such a data set does not contain enough information – or the relevant type of information – to draw conclusions with respect to the causal relationship between the two variables; either could be the cause of the other. Moreover, based on such a limited information you cannot even determine whether relatedness is necessary or sufficient for sociality. The data does not simply contain the relevant sort of variation to serve as a basis for answering such questions. However, the larger, blue area does contain one interesting contrast: the one between the level of relatedness and the level of social behaviour. What such a data set would now clearly suggest is that high relatedness is necessary for social behaviour: only in cases of high relatedness do we also encounter high levels of social behaviour. But to interpret that dependency in causal terms we would need to supplement the data with further, more encompassing information.

Figure 2 gives a schematic representation of the phylogenetic relationship of several taxa of interest, based on the evolutionary scenario discussed in the previous section. This figure represents a simplified version of the actual situation we are facing in the current debate, and the presented data contains enough variation for us to reach some tangible conclusions. What we are now interested in is the relationship of three variables, relatedness, eusociality and an indeterminate variable *X* representing a factor with some potential influence to the emergence of eusociality. For simplicity, each of these variables are treated as binary, with "+" representing the presence of the given feature, and "-" its absence. What the figure suggests is that there is some significant connection between both relatedness and eusociality, and *X* and eusociality.

The debate on the role of relatedness in the evolution of eusociality boils now down to the following question: is the value of the eusociality variable dependent on the value of the relatedness variable or on the value of the *X* variable? A moment's inspection should make it clear that eusociality is actually dependent on both relatedness and *X*, but with an important qualification: the presence of both relatedness and *X* are necessary for the presence of eusociality, but only together they are sufficient. Importantly, relatedness alone is not sufficient for eusociality (the solid red taxa), but only adding *X* makes it appear. And it is exactly this observation, it seems, in which the idea that relatedness has no causal role to play in the evolution of eusociality is rooted. Inspecting the figure 2 helps us to decipher what's right and what's wrong with this idea.

Let us look at some of the concrete claims made by the critics of the kin selection theory and see how they fare in the light of the figure 2. Wilson (2008) claims that "[c]lose genetic relatedness and collateral kin selection are not necessary" (p. 22) for the evolution of eusociality. This is unequivocally false. Many of the critical statements suggest either that high relatedness and eusociality are not connected at all or that eusociality is a cause of high relatedness rather than the other way around. For example, Nowak (2010) claims that "relatedness is better explained as the consequence rather than the cause of eusociality" (p. 1060). None of these claims are supported by the preceding analysis. Firstly, there is a clear connection between relatedness and eusociality: the former is necessary for the latter. Secondly, nothing in figure 2 suggests that eusociality would be the cause of high relatedness. On the contrary: the taxa represented by solid red lines suggest that the presence of high relatedness is not dependent on the presence of eusociality.

However – and this is crucial – figure 2 illustrates also clearly where some of the critical claims gain their credibility. Sometimes it is claimed that high relatedness is not a “salient” feature, or a “driving force” in the evolution of eusociality. For example, Wilson & Hölldobler (2005) claim that “eusociality cannot arise without the driving force of group selection, regardless of the degree of relatedness within local populations or cooperative aggregations” (p. 13367). And Nowak *& al.* (2010) claim that evidence has began to accumulate that is “unfavorable to the basic idea that relatedness is a driving force for the emergence of eusociality” (p. 1058). These claims can actually now be interpreted to be true, at least partly. It is evident from the figure 2 that the presence of eusociality is not dependent on the presence of high relatedness: there are taxa (solid red line) where relatedness is high but eusociality is absent.

Most importantly, note that if you limit your focus on the taxa where high relatedness is present (both solid and dashed red lines) both the presence and absence of eusociality become dependent solely on *X* (this compares to the data set delineated by the red rectangle in figure 1). The phylogenetic reconstructions of relatedness level show that high relatedness (achieved through single mating of the mother) is the ancestral state for eusocial evolution (Hughes *& al.* 2008). As a reference group with low relatedness is typically not available (*e.g*. Hunt 1999), the causal role of relatedness cannot be determined by the data; high relatedness simply appears as a uniform background condition. In such cases it might seem natural to conclude that it is *X* (which could be any of the more salient traits outlined by Hunt (1999)), rather than relatedness, that is the cause of eusociality. But that is simply because the relatedness variable is being held constant (present). If the data does not contain variation in its value, no information is available to ground causal claims on it (neither for nor against the causal efficacy of relatedness).

Thus, for an unequivocal assessment of the causal role of relatedness, these reconstructions alone are clearly not enough. However, data from bees where social behavior is highly variable even among closely related taxa, and variation in relatedness does not derive from mating frequencies but from whether social groups are communal or mother-offspring based, data does suggest that eusocial societies have only developed from the latter, *i.e.* under high relatedness (Danforth 2002). Similarly, in snapping shrimps, phylogenetic contrasts show that eusociality has only evolved in groups where lack of dispersal of larval individuals creates family groups where helping behavior is benefiting closely related individuals (Duffy & Macdonald 2009). Such groups, where the ecological context is invariable, but relatedness varies (figure 2B) have more power to demonstrate the necessary role of relatedness. However, this data does not contain the relevant information to assess precisely the causal role of ecological factors.

Since nature is multifactorial it makes all the difference in the world how you choose to limit your focus, and what you count in and what you leave out from your analysis. If you take all the available empirical data into account, it becomes apparent that high relatedness is necessary, but not (by itself) sufficient for eusociality. From figure 2 it is easy to see – when all the information present in the figure is taken into account – that when relatedness is absent, eusociality will also be absent; the former is therefore necessary for the latter. But it is equally easy to see that when relatedness is present it is not necessarily so that eusociality will also be present; the former is therefore insufficient for the latter. However, it would be wrong to conclude from this that it is *X* rather than high relatedness that is causally related to eusociality. According to the evidence presented in figure 2, *X* is causally related to eusociality only on the condition that high relatedness is present. In other words, although high relatedness by itself appears to be insufficient for eusociality, together with *X* they form a sufficient whole: high relatedness added with *X* brings about eusociality. But such a conclusion is perfectly in line with the received view on the evolution of eusociality.

## 5. Conclusions

Both theoretical and empirical considerations suggest an indispensable role for relatedness in the evolution of eusociality, but relatedness seems to enter the picture as a necessary condition. It is thus not clear how the seemingly provocative statements about the causal role of relatedness should be interpreted. Much depends on the more general question of how one perceives the causal status of natural selection in the process of evolution. If one subscribes to the view that natural selection is the primary causal mechanism in evolution, then one is bound to accept the view that relatedness has played a causal role in the evolution of eusociality, as a necessary element of natural selection. This view does not require that relatedness is a trait with high salience with respect to the evolution of eusociality. If, on the other hand, one sees the evolution by natural selection wholly statistically and consequently disavows the causal role of natural selection in evolution, then one is bound to deny the causal role of relatedness in the evolution of eusociality. However, such a conclusion would follow trivially from the adopted philosophical view on the role of natural selection in evolution and would thus not be very informative (at least not in the way the critics suggest).

While the role of causal explanation in the theory of social evolution is an issue that has been addressed by some recent discussions (Allen *& al.* 2013; Birch & Okasha 2014; Okasha 2006) it is worth stressing that our conclusions complement these earlier discussions in important respects. Although questions on whether kin selection or multilevel selection models of social evolution are formally equivalent, and on whether the one or the other offer a more adequate causal description of the evolutionary process, are highly pertinent, our aim here is to highlight the fact that as long as pedigree relatedness is underlying the heritability of phenotypes, in the way outlined here, giving a definite answer to questions concerning the causal role of relatedness in the evolution of eusociality depends more on one's view on causal explanation in the theory of evolution in general, rather than on the choice of modeling methods.

The fact that relatedness is a necessary condition for the evolution of eusociality does not by itself dictate a particular, unequivocal conclusion in causal terms. Whether necessary conditions are interpreted causally depends on the larger context in which such conditions are embedded. If the relatedness variable in a data set is held at a uniformly high value, then it indeed turns out that other factors become to occupy a more salient role. Since the received view on the evolution of eusociality holds only that high relatedness is necessary for the evolution of eusociality, it is perfectly consistent with this to hold that other factors will also need to be present to make eusociality actually appear. Since both high relatedness and additional factors need to be present, and they play logically distinct roles depending on different ways of delineating the relevant data, in certain situations it can actually be perfectly cogent to claim that other factors than high intracolonial relatedness appear to drive the evolution of eusociality. However, this does not change the fact that high relatedness functions as a necessary background condition for the process, and that kin selection theory is an indispensable tool for understanding the evolution of eusociality.

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## References

Abbott, P.E. *& al.* (2011). “Inclusive fitness theory and eusociality”. *Nature* 471, p. E1-E4.

Allen, Benjamin, Nowak Martin A. & Wilson, Edward O. (2013). “Limitations of inclusive fitness”. *Proceedings of the National Academy of Sciences of the United States of America* 110, p. 20135–20139.

Bijma, P. (2011). “A general definition of the heritable variation that determines the potential of a population to respond to selection”. *Genetics* 189, p. 1347-1359.

Birch, Jonathan (2014). “Hamilton’s rule and its discontents”. *British Journal for the Philosophy of Science* 65, p. 381-411.

Birch, Jonathan & Okasha, Samir (2014). “Kin selection and its critics”. *BioScience* 65, p. 22–32.

Boomsma Jacobus J., Beekman M., Cornwallis C.K., Griffin A.S., Holman L., Hughes W.O.H., Keller L., Oldroyd B.P., Ratnieks F.L.W. (2011). “Only full-sibling families evolved eusociality”. *Nature* 471, p. E4-E5.

Boomsma, Jacobus J. & Gawne, Richard (2017). “Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation”. *Biological Reviews*.

Bourke, A.F.G. (2011). *Principles of Social Evolution*. Oxford: Oxford University Press.

Buschinger, A. (2009). “Social parasitism among ants: a review (*Hymenoptera*: *Formicidae*)”. *Myrmecological News* 12, p. 219-235.

Cummins, Robert (1975). “Functional analysis”. *Journal of Philosophy* 72, p. 741-765.

Danchin, E., Charmantier, A., Champagne, F.A., Mesoudi, A., Pujol, B., Blanchet, S. (2011). “Beyond DNA: integrating inclusive inheritance into an extended theory of evolution”. *Nature Reviews Genetics* 12, p. 475-486.

Danforth, Bryan N. (2002) “Evolution of sociality in a primitively eusocial lineage of bees”. *Proceedings of the National Academy of Sciences* 99, p. 286-290.

Dretske, Fred (1990). “Reply to reviewers”. *Philosophy and Phenomenological Research* 50, p. 819-839.

Duffy, J. Emmett, & Macdonald, Kenneth S. (2009). “Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis”. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb2009.1483.

Futuyma, Douglas J. (2005). *Evolution*. Sunderland MA: Sinauer Associates.

Gadagkar, R. (1990). “Evolution of eusociality - the advantage of assured fitness returns”. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 392, p. 17-25.

Gardner, A. & Grafen, A. (2009). “Capturing the superorganism: a formal theory of group adaptation”. *Journal of Evolutionary Biology* 22, p. 659–671.

Gould, Stephen J. & Lewontin, Richard C. (1979). “The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme”. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 205, p. 581-598.

Hamilton, W.D. (1964). “Genetical evolution of social behaviour i”. *Journal of Theoretical Biology* **7**, p. 1-16.

Helanterä, Heikki (2016) “An organismal perspective on the evolution of insect societies”. *Frontiers in Ecology and Evolution* 4, 6.

Helanterä, Heikki & Bargum, Katja (2007). “Pedigree relatedness, not greenbeard genes, explains eusociality”. *Oikos* 116, p. 217-220.

Helanterä, Heikki & Uller, Tobias (2010). “The Price Equation and extended inheritance”. *Philosophy and Theory in Biology* 2, p. 1-17.

Hunt, James H. (2011). “A conceptual model for the origin of worker behaviour and adaptation of eusociality”. *Journal of Evolutionary Biology* 25, p. 1-19.

Hunt, James H. (1999). “Trait mapping and salience in the evolution of eusocial *Vespid* wasps”. *Evolution* 53, p. 225-237.

Hunt, James H & Amdam, Gro V. (2007). “Bivoltinism as an antecedent to eusociality in the paper wasp genus *Polistes*”. *Science* 308, p. 264-267.

Liao, Xiaoyun, Rong, Stephen & Queller, David C. (2015). “Relatedness, conflict, and the evolution of eusociality”. *PLOS Biology* 13, e1002098.

Linksvayer, T.A. & Wade, M.J. (2009). “Genes with social effects are expected to harbor more sequence variation within and between species”. *Evolution* 63, p. 1685-1696.

Marshall, J.A.R. (2015). *Social Evolution and Inclusive Fitness Theory: An Introduction.* Princeton: Princeton University Press.

Mayr, Ernst (1982). *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge MA: Harvard University Press.

Mackie, John L. (1965). “Causes and conditions”. *American Philosophical Quarterly* 12, p. 245-265.

Mackie, John L. (1974). *The Cement of the Universe: A Study of Causation*. Oxford: Oxford University Press.

McGlothlin, J.W., Moore, A.J., Wolf J.B., Brodie E.D. (2010). “Interacting phenotypes and the evolutionary process. III. Social evolution”. *Evolution* 64, p. 2558-2574.

Neander, Karen (1995). “Pruning the tree of life”. *British Journal for the Philosophy of Science* 46, p. 59-80.

Nowak, Martin A. & Allen, Benjamin (2015). “Inclusive fitness theorizing invokes phenomena that are not relevant for the evolution of eusociality”. *PLOS Biology* 13, e1002134.

Nowak, Martin A., Tarnita, Corina E., Wilson, Edward O. (2010). “The evolution of eusociality”. *Nature* 466, p. 1057-1062.

Nowak, Martin A., Tarnita, Corina E., Wilson, Edward O. (2011). “Nowak & al. reply”. *Nature* 471, E9-E10.

Okasha, Samir (2006). *Evolution and the Levels of Selection*. Oxford: Oxford University Press.

Pigliucci, Massimo & Müller, Gerd B. (eds.) (2010). *Evolution: The Extended Synthesis*. Cambridge MA: MIT Press.

Queller, David C. (1989). “The evolution of eusociality: reproductive head starts of workers”. *Proceedings of the National Academy of Sciences of the United States of America* 86, p. 3224-3226.

Queller, David C. (1994). “Extended parental care and the origin of eusociality”. *Proceedings of the Royal Society of London Series B-Biological Sciences* 259, p. 105-111.

Queller, David C. (2011). “Expanded social fitness and Hamilton's rule for kin, kith, and kind”. *Proceedings of the National Academy of Sciences* 108, p. 10792-10799.

Queller, David C. & Strassmann J.E. (1998). ”Kin selection and social insects”. *BioScience* 48, p. 165-175.

Ratnieks, F. L. W., K. R. Foster, & T. Wenseleers. (2006). “Conflict resolution in insect societies”. *Annual Review of Entomology* 51, p. 581-608.

Ratnieks, Francis L.W. & Helanterä, Heikki (2009). “The evolution of extreme altruism and inequality in insect societies”. *Philosophical Transactions of the Royal Society B-Biological Sciences* 364, p. 3169-3179.

Reisman, Kenneth & Forber, Patrick (2005). “Manipulation and the causes of evolution”. *Philosophy of Science* 72, p. 1113-1123.

Ross, L., Gardner, A., Hardy, N. & West, S.A. (2013). “Ecology, not the genetics of sex determination, determines who helps in eusocial populations”. *Current Biology* 23, p. 2383-2387.

Rousset, F. & Lion, S. (2011). “Much ado about nothing: Nowak et al.'s charge against inclusive fitness theory”. *Journal of Evolutionary Biology* 24, p. 1386-1392.

Schwander, T., N. Lo, M. Beekman, B. P. Oldroyd, & L. Keller (2010). “Nature versus nurture in social insect caste differentiation”. *Trends in Ecology & Evolution* 25, p. 275-282.

Sober, Elliott (1984). *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Cambridge MA: MIT Press.

Sober, Elliott (1995). “Natural selection and distributive explanation: a reply to Neander”. *British Journal for the Philosophy of Science* 46, p. 384-397.

Toth, A.L., Varala, K., Newman, T.C., Miguez, F.C., Hutchison, S.K., Willoughby, D.A., Simons, J.F., Egholm, M., Hunt, J.H., Hudson, M.E., Robinson, G.E. (2007). “Wasp gene expression supports an evolutionary link between maternal behavior and eusociality”. *Science* 318, p. 41-44.

Van Zweden, J., Cardoen, D., Wenseleers (2012) “Social evolution: when promiscuity breeds cooperation”. *Current Biology* 22, p. R922-R924.

Walsh, Denis M., Lewens, Tim & Ariew, André (2002). “The trials of life: natural selection and random drift”. *Philosophy of Science* 69, p. 452-473.

West, S. A., A. S. Griffin, & A. Gardner. 2007. “Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection”. *Journal of Evolutionary Biology* 20, p. 415-432.

West-Eberhard, M.J. (2003). *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

Wilson, Edward O. (2008). “One giant leap: how insects achieved altruism and colonial life”. *BioScience* 58, p. 17-25.

Wilson, Edward O. (2014). *The Meaning of Human Existence*. New York: Liveright.

Wilson, David S. & Wilson, Edward O. (2007). “Rethinking the theoretical foundation of sociobiology”. *Quarterly Review of Biology* 82, p. 327-348.

Wilson, Edward O. & Hölldobler, Bert (2005). ”Eusociality: origin and consequences”. *Proceedings of the National Academy of Sciences of the United States of America* 102, p. 13367-13371.

Wilson, Edward O. & Nowak, Martin A. (2014). “Natural selection drives the evolution of ant life cycles”. *Proceedings of the National Academy of Sciences of the United States of America* 111, p. 12585–12590.

Figure 1

A hypothetical example of how the context where a question is framed affects causal conclusions, when relatedness and social behaviour are continuous variables. Data in red rectangle (red line for correlation) support the hypothesis that relatedness is not sufficient, and it is impossible tell whether relatedness is necessary as relatedness is uniformly high. Data in blue rectangle (blue line for correlation) support a necessary, but not sufficient role for relatedness, and shows a correlation with a possible causal interpretation.

Figure 2A

A hypothetical example of how the context where a question is framed affects causal conclusions, when relatedness and social behaviour are binary variables. The part of the phylogeny denoted by a dashed red line does not demonstrate an association with eusociality for neither single mating nor *X*. The part denoted by a dashed and solid red lines shows an association between *X* and eusociality, but not between single mating and eusociality. The total phylogeny, denoted by a dashed and solid red lines together with the blue lines shows both single mating and *X* to be associated with eusociality, with *X* being more salient. The full data set suggests that single mating and *X* are both necessary, and that their co-occurrence is sufficient for eusociality. *X* could here be any of the traits Hunt (1999) describes as highly salient for eusociality. However, in the phylogenetic reconstructions, the absence of a sister group with low relatedness caused by multiple mating (blue lines) for comparison makes assessing role of relatedness difficult. This is similar to the situation described by Hunt (1999).

Figure 2B

(Modified from Duffy & Macdonald 2009.) Data from Synalpheus shrimps shows that high relatedness brought by non-dispersal of larvae is necessary for eusociality (red branches) whereas the necessity of *X* (representing the ecological setting where eusociality has been suggested to be beneficial) cannot be analysed with this data. *M* = missing data.