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Group and individual selection during evolutionary transitions in individuality: meanings and partitions

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The Price equation embodies the 'conditions approach' to evolution in which the Darwinian conditions of heritable variation in fitness are represented in equation form. The equation can be applied recursively, leading to a partition of selection at the group and individual levels. After reviewing the well-known issues with the Price partition, as well as issues with a partition based on contextual analysis, we summarize a partition of group and individual selection based on counterfactual fitness, the fitness that grouped cells would have were they solitary. To understand 'group selection' in multi-level selection models, we assume that only group selection can make cells suboptimal when they are removed from the group. Our analyses suggest that there are at least three kinds of selection that can be occurring at the same time: group-specific selection along with two kinds of individual selection, within-group selection and global individual selection. Analyses based on counterfactual fitness allow us to specify how close a group is to being a pseudo-group, and this can be a basis for quantifying progression through an evolutionary transition in individuality (ETI). During an ETI, fitnesses at the two levels, group and individual, become decoupled, in the sense that fitness in a group may be quite high, even as counterfactual fitness goes to zero.

This article is part of the theme issue 'Fifty years of the Price equation'.

1. Introduction

Natural selection occurs in populations of entities that can multiply and that have heritable variation in traits that affect the probability of multiplying. In short, these entities have heritable variation in fitness. Succinct summaries of conditions that result in evolution by natural selection trace back to Darwin, though many others have since refined this 'conditions approach' to conceptualizing natural selection [1].[1] The conditions that embody natural selection are applicable to a variety of kinds of entities, including individuals and groups of individuals, and this basic observation is the basis for research into multi-level selection (MLS). Much MLS research has focused on issues of altruism, cooperation and conflict, given two clearly established hierarchical levels of organization. Another thread of inquiry asks how one is to understand natural selection as a new level of selection, or evolutionary individual, first emerges and then becomes established [5–15]. The latter kind of situations are known as evolutionary transitions in individuality (ETIs), where 'individual' is meant to refer to different kinds of entities or units of selection, such as gene replicators, protocells, simple bacteria-like cells, eukaryotic cells, multicellular organisms or eusocial societies. The two research areas are related but distinct in their focal questions and assumptions.

In this paper, we first review the conditions approach to selection in group-structured populations, especially as it is manifest in the Price equation. We then briefly contrast the Price/conditions approach to partitioning levels of selection with an alternative approach known as contextual analysis. Next, we describe our own partition based on counterfactual fitness, the fitness an

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entity would have had, had it not been a member of a group (or, equivalently, had it existed in a pseudo-group). Our analyses based on counterfactual fitness are motivated by studies of selection in the volvocine green algae, a model system for ETIs. We assume that selection must act at the group level in order to produce traits such that, were the entity to leave the group, the trait would reduce rather than enhance fitness (as long as stochastic and linked-loci effects are absent). To put it another way, we assume that if selection takes place purely at the lower, individual, level, then it will adapt traits for solitary life. Only when group-level selection is in effect will traits appear that adapt an entity for group life at the expense of solitary autonomy. The hypothetical existence of pseudo-groups, groups that satisfy Darwin's conditions but only for reasons related to solitary fitness, has been a problematic case in the discussion of selection in group-structured populations. As we show in equation (4.1), counterfactual fitness allows us to quantify just how close a group is to being a pseudo-group. Two meanings of 'individual selection' are salient in our model because counterfactual fitness separates a potentially non-zero partition of 'individual selection' even when within-group (individual) selection is assumed to be absent. The issue of multiple meanings of individual selection is the flip side of the two incompatible meanings of 'group selection' that have been discussed in reference to Price and contextual partitions. Finally, we discuss the issue of 'progression' through an ETI and relate this to the issues of counterfactual fitness and identifying and partitioning levels of selection. During ETIs, fitness at the two levels, group and individual, become decoupled, in the sense that the fitness of the group may be quite high, even as counterfactual fitness goes to zero. We conclude by discussing our main points.

2. The Price equation in group-structured populations

The Price equation or Price's theorem [16,17] can be thought of as a mathematical version of the conditions approach to natural selection [14, pp. 36–37]. It is characterized by simplicity and broad scope, and many see it as fundamental (e.g. [18,19]). Using notation from Frank [20], the Price equation is

$$\Delta z = \sum (\Delta q_i) z_i + \sum q'_i (\Delta z_i), \tag{2.1}$$

where Δz is the change in the average value of a trait between two populations, which we assume to be an ancestral and a descendent population. The trait value of a type of individual in the first population is z_i, while z'_i denotes the average trait value in the descendants, and Δz_i is the difference of these two values. The proportion of the ancestral population that is i-type is given by q_i, the proportion of the descendent population with i-type ancestors is q'_i and Δq_i is the difference of these two values. The left-hand side (l.h.s.) of the equation is the total change in average trait value between an ancestor and a descendent population.

The fitness of a type, w_i, is defined according to the equation $q'_i = q_i(w_i/w)$. With this definition, the first right-hand side (r.h.s.) term is often written as $\mathrm{Cov}(w, z)/w$ and interpreted to mean the change in the average trait value that is due to natural selection. In the case with no property change, $\Delta z = \mathrm{Cov}(w, z)/w$. This is known as the Robertson–Price identity [21, p. 151] because Robertson [22] and Price [16] independently presented it. The second term on the r.h.s. is often written as $E(w\Delta z)/w$. It is the fitness-weighted average change in trait values from ancestor to descendants. It is often described as the change in the average trait value that is due to property change or transmission bias. See Walsh & Lynch [21, p. 149] for alternative partitions, and see Okasha [23] and Godfrey-Smith [1] for discussion of a three-category partition that can be seen as separating the interaction between property change and selection.

Because the logic of natural selection is so general, it can apply to different hierarchically nested levels; this is known as multi-level selection (MLS). Price [17] and Hamilton [24] showed how the Price equation can be applied recursively to represent selection at different levels. The standard Price equation partition can be written as follows:

$$\Delta z = \frac{\mathrm{Cov}_i(w_i, z_i)}{w} + \frac{E_i[w_i \Delta z_i]}{w}. \tag{2.2}$$

Now assume that the trait change of interest, Δz, is occurring in a population whose entities contain within them lower-level populations. So, Δz is the average trait change in a population of groups, and each ancestral group is indexed by i. We can take the Δz_i from the second term in the r.h.s. of equation (2.2) and use it as a starting point for a Price partition within each of the i groups. The trait value at the group level is assumed to be the average of the trait values at the lower level and likewise for fitness. We use the index j to denote entities within the groups, and we get

$$\Delta z = \frac{\mathrm{Cov}_i(E_j[w_{ij}], E_j[z_{ij}])}{w} + \frac{E_i[\mathrm{Cov}_j(w_{ij}, z_{ij})]}{w} + \frac{E_{ij}[w_{ij}\Delta z_{ij}]}{w}. \tag{2.3}$$

See Frank [25], Wade [26] or Price [17] for details of this derivation. The first r.h.s. term in equation (2.3) is the same as in equation (2.2), but it is written differently to emphasize that the higher-level parameters are averages of the lower-level parameters. The r.h.s. of equation (2.3) has three terms: (i) the trait change that is often attributed to group-level selection, (ii) the average over all the groups of the changes due to within-group selection, and (iii) the transmission bias or property change of the particles themselves. The third term is often assumed to be zero in multi-level Price equation applications. Hamilton [24] interpreted equation (2.3) as accomplishing a 'formal separation of levels of selection'. Unfortunately, further analysis of the Price partition discussed below have shown the situation is not so simple, and different partitions are needed to formally separate group and individual selection in explicit models of group-structured populations.

Having introduced the Price equation and its multi-level partition in equation (2.3), in §3 'Price versus contextual partitions of multi-level selection', we compare the Price approach with that of contextual analysis in terms of partitioning the levels of selection. We provide a brief summary of 'problem cases' that have been observed for each approach. A problem case for the Price approach is that of spurious correlations that cross hierarchical levels, and this issue is a lens that we used in analysing algae-inspired models of early stages in an ETI [27,28]. We describe these models based on counterfactual fitness in §4 'Selection in the context of homogeneous groups'. We then consider in §5 'Meanings of individual selection and group selection', how these models of homogeneous groups and other models allowing both within-group and between-group variation (conflict mediator models) can inform distinctions between different meanings of 'group selection' and 'individual selection'. In §6 'Evolutionary transition in individuality progression and meanings and partitions of group and individual selection', we connect these different meanings and partitions of group and individual selection to the question of how to quantify progression through an ETI.

3. Price versus contextual partitions of multi-level selection

Okasha [4] describes two main alternative ways one could partition total change in a trait value into a sum of terms corresponding to group-level and individual-level selection. One possibility is to use the Price approach with the assumption that the lowest level in the hierarchy is transmitted perfectly (i.e. equation (2.3) with the third r.h.s. term set to zero). The second possibility, contextual analysis, treats the individual's characteristic (z_{ij}) and the characteristic of the group the individual belongs to (Z_j) as independent variables in a linear regression model of individual fitness (w_{ij}) [29–31]. Also see Nunney [32,33], Goodnight *et al.* [29], Okasha & Paternotte [34], Earnshaw [35] and Bourrat [36] for more on contextual analysis and the related neighbour approach. The total trait change can be decomposed as follows:

$$\Delta z = \frac{\beta_1 \mathrm{Var}(z_{ij})}{w} + \frac{\beta_2 \mathrm{Cov}(z_{ij}, Z_j)}{w}, \qquad (3.1)$$

where β_1 is the partial regression coefficient of individual fitness on individual character and β_2 is the partial regression coefficient of individual fitness on group character. Both of these possibilities (Price and contextual partitions) reflect the idea that group-level and individual-level selection are evolutionary 'forces' with separable, additive effects on overall trait change. Both are mathematically valid ways of partitioning the total change. However, they are different partitions, so they cannot both have a valid claim of separating the effects of group-level selection and individual-level selection. Based on this kind of reasoning, Okasha [4] examined problem cases for each partition and concluded that neither has an unequivocally strong claim to effecting a 'formal separation of levels of selection' as Hamilton sought [24].

For contextual analysis, one problem case is that known as soft selection. This is a situation in which there is variation in individual fitness, but there is not variation in group fitness. Contextual analysis will detect non-zero group selection in this case (whereas the Price partition will not). Okasha [4, p. 96] notes that 'the idea that selection at a level requires variance in fitness at a level is virtually axiomatic', so many see it as a problem that contextual analysis detects group selection when groups do not vary in fitness.[2] Analysis of the contextual versus Price partitions has brought to the fore two mutually incompatible meanings of 'group selection'. Earnshaw [35, p. 309] puts it this way: 'The key issue is whether "group selection" refers to the effect of interactions between members of a group, or whether it refers to variation in overall group productivity'. Sober [38, p. 836] describes the distinction this way: 'For the contextual approach, "group selection" means that an individual's fitness is affected by the kind of group the individual occupies. For the Price approach, "group selection" means that there is variation in the fitnesses of groups'. We return to the issue of distinct meanings of 'group selection' and 'individual selection' in §5 'Meanings of group selection and individual selection'.

For the Price equation, one problem case concerns the issue of spurious correlations, correlations that are not reflective of a direct causal link between two variables. The covariance term in the Price equation, $\mathrm{Cov}_i(w_i, z_i)/w$ could reflect a spurious correlation. Consider two traits (e.g. coloration and weight) that are correlated with each other in a particular population. One trait (e.g. coloration) causes changes in fitness and thus is correlated with fitness. The other trait (e.g. weight) can be expected to have a non-zero correlation with fitness even though there is not a direct cause–effect relationship between this trait and fitness. Even in a single-level scenario, it cannot be taken for granted that a non-zero value of $\mathrm{Cov}_i(w_i, z_i)/w$ is the change caused by selection on that trait. The distinction between spurious versus causal correlations has been referred to as 'selection of' the correlated trait versus 'selection for' the trait that causes fitness differences [39, pp. 97–102] and indirect versus direct selection. Although spurious correlations may be an issue in a single-level Price analysis, they do not generally pose difficult conceptual challenges. Spurious correlations become more of a problem for a Price approach to multi-level scenarios.

If an investigator designates arbitrary, biologically meaningless groups which differ in their composition (i.e. some groups have lots of high-fitness individuals and some groups do not), then group-level fitness will covary with group-level traits. We call these pseudo-groups, following Godfrey-Smith & Kerr [40]. For example, given individual-level directional selection on deer speed, pseudo-group herds of deer with high average running speed would do better than herds with low average running speed. The Price partition will detect group selection in such a case, even if it is only the speed of the individual deer and not the average speed of the herd that actually matters. That is, the Price partition disagrees with the intuition that this is an example of individual-level selection. Williams [41], prior to the publication of the Price equation, called this kind of issue a 'fortuitous group benefit'. See Okasha [42], Godfrey-Smith & Kerr [40] and Okasha [4, p. 78] for more on pseudo-groups and related issues.

Sober & Wilson [43] side-step the issue of fortuitous group benefits in pseudo-groups by adhering to a Price approach but disallowing arbitrary designations of groups. They define groups based on fitness-affecting interactions.[3] This move has the consequence that arbitrarily tiny group effects can change a situation from being one of zero group selection to one of extremely strong group selection. Okasha [4, p. 97] finds this to be problematic. Also, see Sober [46] for related discussion. If we agree that the pseudo-group case is a case of individual selection, then there is an appeal to the idea that the effects of individual selection would gradually fade out as we gradually tweak the scenario (by continuously introducing a group effect). But if we assume that 'group selection' is fading in as 'individual selection' fades out, then this desideratum is in essence changing the meaning of 'group selection' to line up more with the contextual analysis meaning of group selection (i.e. that it is essentially about group effects on individuals as opposed to a more traditional group-level 'conditions' meaning).

The issue of cross-level spurious correlations comes up in our analysis of models that were primarily aimed at capturing how a group-level life cycle can emerge and become entrenched early in an ETI [27,28]. Based on the biology of our algal model system, we restricted our focus to groups that can be assumed to be homogeneous. In essence, these are not MLS models. Selection can be analysed at the group or individual level, but not both simultaneously. Nevertheless, our model showed how trait change could be book-ended by situations of 'individual selection' (in which the correlation between group trait and group fitness is entirely spurious) and 'group selection' (in which group traits genuinely and strongly contribute to group reproductive success) with a gradual shift in between. That this can occur when within-group selection (the traditional meaning of 'individual selection') being zero leads us to conclude that more attention should be paid to distinguishing distinct meanings of individual and group selection. In the next section, we describe these homogeneous group models as a basis for further discussion about meanings and partitions of levels of selection.

4. Selection in the context of homogeneous groups

Here, we summarize models of an early-stage ETI based on the biology of the volvocine algae (*Volvox* together with its simpler colonial and unicellular relatives). In the volvocine algae, the earliest-branching colonial species (such as *Basichlamys* and *Tetrabaena* in the family Tetrabaenaceae) have a small number of cells per colony and a single-celled bottleneck during development. The single-cell bottleneck in particular seems a natural extension of a mode of cell growth and division known as palintomy or multiple fission that is also characteristic of unicellular volvocine algae. The unicellular volvocine algae undergo multiple fission, growing about 2^n-fold before rapidly dividing n times to produce offspring cells. A small change to this cell cycle (i.e. temporary adhesion of offspring cells) makes it a group life cycle with a single-cell bottleneck [27,28]. We focus on the asexual multicellular stage of the life cycle here, though volvocine algae also undergo sex in response to stress.

A single-cell developmental bottleneck and a fixed group size can evolve through group-level selection, because they suppress within-group selection [13,47–51]. See appendix A for further description of these conflict mediation models. It is also plausible that the earliest volvocine algae could have had features such as a single-cell bottleneck as 'holdovers' from their unicellular biology. That is, there may be an initial phase in the volvocine ETI during which low-conflict colonies emerge 'for free', without the need for specific conflict mediation adaptations.

Because of the single-cell bottleneck and small number of cells per group, it is a reasonable approximation to consider early-branching volvocine groups to be homogeneous and to ignore the effects of within-group selection. Beginning with that assumption, we developed a model concerning the evolution of a cell-level life-history trait that is basic to cell fitness, allocation to cell growth, g [28]. We explored a way to operationalize the idea that the magnitude of group selection should be related to the magnitude of group effects on fitness. Because the groups are assumed to be homogeneous, we could not simply turn to contextual analysis. The relevant partial regression coefficients (see equation (3.1) and surrounding text) are not defined if all of the individuals (cells) with a given individual characteristic (value of g) also have the same group/contextual characteristic (group's average g).

We first considered the optimality of the trait, g, in the unicellular context, where it was adaptive for a unicell to have an intermediate trait value because of a trade-off. Higher values of allocation to growth, g, increased cell fitness via its effects on the cell growth rate but decreased cell fitness via its effects on the cell mortality rate. The unicellular cell cycle under consideration means that little needs to change for a group life cycle to get started.[4] After analysing the unicellular case, we considered cases where cells were fixed for a small life cycle change that created groups (i.e. in the group cases, cells were assumed to stay together for some time after divisions). We considered both the case when the groups have no effect (pseudo-groups) and the case when being in a group does affect the optimality of the allocation to growth trait. In the latter case, alongside the suite of effects that constituted cell-level selection on g in the pseudo-group case, a genuine group effect of g was posited. In our model, the size (cell number) of the colony was assumed to directly affect cell mortality, with cells belonging to larger colonies experiencing reduced mortality. This is analogous to the example raised in Sober [38, p. 838], where 'lions decide which zebra herds to attack by assessing the herd's average running speed'. Parameters in the model could be adjusted to make this group-level effect arbitrarily small, meaning the entire scenario could be set arbitrarily close to the 'no effect' (i.e. individual selection, pseudo-group) case. Whether the groups have a minuscule effect on the optimality of g, allocation to growth, or whether they have a huge effect, the conditions approach to natural selection (and thus the standard Price partition) alone would identify this as a case of only group selection (because there is no within-group variation).

In order to quantify 'how close' a scenario is to the pseudo-group (i.e. individual selection) case, we defined Ω as the counterfactual fitness.[5] Counterfactual fitness is the fitness that a cell would have if it had the same cell-level traits but existed in a global population of cells (or, equivalently, a pseudo-group) rather than within a meaningful group structure. In the pseudo-group case, counterfactual fitness equals realized fitness. That is, the groups do not matter, so if one were to separate group members, no effect on individual fitness would be observed. What if one were to separate cells and a change in cell fitness was observed? In our scenario, it would be reasonable to attribute this difference to group selection. In the pursuit of greater clarity about MLS itself, our scenario sets aside many complications such as stochastic effects and linked traits. Specifically, we found that (converting eqn (9) of Shelton & Michod [28] to the notation of equations (2.1)–(2.3) and (3.1))

$$\Delta z = \frac{\mathrm{Cov}(\Delta w_i, z_i)}{w} + \frac{\mathrm{Cov}(V_i, z)}{w}, \qquad (4.1)$$

where Ω is the counterfactual fitness (described previously), z is the trait value (which is g, allocation to growth, in

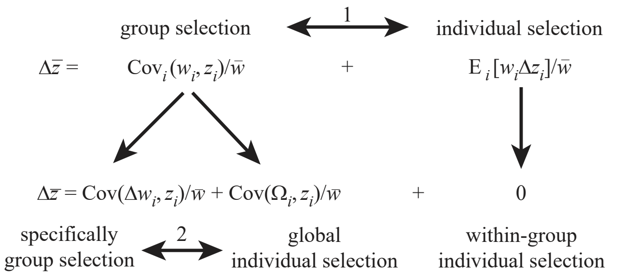

Figure 1. Different meanings of group and individual selection. The top row shows the standard Price equation partition and maps the terms to 'group selection' and 'individual selection'. Here, we are ignoring lower-level property change. The bottom row shows the partition used in Shelton & Michod [28] in their analyses of selection in homogeneous groups, given as equation (4.1), and maps the terms to 'specifically group selection', 'global individual selection' and 'within-group individual selection'. The horizontal double arrows indicate two contrasts that are emphasized in the text and in table 1: (1) the group selection versus within-group selection contrast, and (2) the contrast between specifically group selection and global individual selection.

Shelton & Michod [28]; we use z here for notational consistency) and Dw is the difference between relative fitness and counterfactual relative fitness. The second r.h.s. term is the trait change that would have happened in a population of pseudo-groups. The first r.h.s. term is the additional trait change that can be attributed to group-dependent trait–fitness relationships. The index i refers to groups in equation (4.1) (eqn (9) in Shelton & Michod [28]). However, because we are focusing on homogeneous groups, indexing groups or individuals is a matter of perspective only. Fitness accounting can be done at either level (see eqns (30) and (36) in Shelton & Michod [28]), but fitness does not vary at both levels simultaneously.

We partitioned change in trait value into a component that would have happened without the group structure, $\mathrm{Cov}(V_i, z_i)=w$, and the remaining trait change $\mathrm{Cov}(Dw_i, z_i)=w$. We consider $\mathrm{Cov}(Dw_i, z_i)=w$ to be a quantification of the trait change that is due to group-dependent cause–effect relationships between the group trait and group fitness. Is $\mathrm{Cov}(Dw_i, z_i)=w$ the 'change due to group selection'? Those who favour the contextual-inspired meaning of 'group selection' might say 'yes', whereas those who favour a Price-inspired meaning of 'group selection' might say 'no'. We called this term 'specifically group-level selection for z' in order to show that there is a logical connection to 'group selection' but that is not the same meaning of 'group selection' that the conditions/Price approach suggests (figure 1 and table 1).

We consider $\mathrm{Cov}(V_i, z_i)\text{Þ}=w$ to be a quantification of trait change due to group-independent cause–effect relationship between the trait and fitness. We called this 'global' individual-level selection for z to contrast it with the meaning of individual selection as based on local within-group differences in fitness (since there are no within-group differences in our model) (figure 1 and table 1). The distinction between global and within-group individual selection has also come up in a debate between MLS conventionalists and realists [46, p. 223]. In our model, we are not bringing up the idea of global individual selection as a way to promote conventionalism about levels of selection, as we predict that both forms of individual selection (within-group selection and global individual selection) could exist in a model at the same time; further exploration of this connection is beyond our scope here.

This model [28] together with a related model [27] show that the constellation of factors that constitute individual selection on a unicellular trait value do not go away with the initial advent of a grouped life stage. In other words, something that might reasonably be called 'individual selection' can still be in operation during the initial stages of an ETI, even if all the fitness variance occurs between rather than within groups. The model also shows how specifically group-dependent effects can interact with life-cycle traits to drive the system towards a fully group life cycle characterized by cells that have a rather different life-history trait value compared with what they would have alone or in a pseudo-group. That is, specifically group selection is important to distinguish from global individual selection because the former can have a role in entrenching a group life cycle.

5. Meanings of individual selection and group selection

In §3, we saw that the Price and contextual partitions can be seen as competing partitions that are connected to distinct meanings of 'group selection'. Here, we re-examine and add to this distinction based on the homogeneous group models described in §4 [27,28] and on the conflict mediation models described in appendix A [13,47–51].

When the Price and contextual approaches are framed as competing partitions of group versus individual selection, the incompatibility of the two meanings of 'group selection' associated with these two approaches is made salient. In the Price/conditions approach, 'group selection' is what happens when there are fitness differences among groups. In the contextual approach, 'group selection' is the additional force that can change individual traits when the group context matters for an individual's success (table 1). In cases of soft selection, when there is no between-group fitness variance, the 'group selection' term of the Price equation is zero, but contextual analysis still can produce a partition with two non-zero terms. In our homogeneous group models, we explored the other extreme, a case in which the individual selection Price term is zero, and still encountered the need for a distinction that is analogous to the one made by the contextual partition. That is, the partition we used to quantify 'how close' to a pseudo-group a scenario is (equation (4.1)) can be thought of as capturing the magnitude of group effect on fitness.[6]

In addition to the two meanings of 'group selection' in the Price and contextual approaches are the two meanings of 'individual selection' discussed above, and keeping these meanings distinct is also critical for understanding group-structured models (figure 1 and table 1). 'Individual selection' in group-structured populations can mean: (1) within-group individual selection or (2) global individual selection (in contrast with the local within-group selection being referred to in the first meaning). By definition, there is no within-group selection in our homogeneous group models, but we see the effects of global individual selection in the second term of equation (4.1). This may at face value seem like a matter of perspective, but our work suggests that this

Table 1. Two meanings of group and individual selection. This table describes two meanings, labelled 'meaning 1' and 'meaning 2' of group and individual selection discussed in the text.

	meaning 1	meaning 2
group selection	—the result of variation in the fitnesses of groups —meaning suggested by Price partition and conditions approach —labelled 'group selection' in figure 1	—the result of group-dependent effects on fitness —meaning suggested by contextual and counterfactual partitions —labelled 'specifically group selection' in figure 1
individual selection	—trait-based frequency changes that play out between lower-level entities within a group; —labelled within-group individual selection in figure 1	—trait-based frequency changes that would play out between lower-level entities in the absence of group-specific effects —labelled global individual selection in figure 1

is not only about alternative perspectives. In the homogeneous group models, meaning 1 (within-group selection) was absent. Yet meaning 2 (global individual selection) is applicable and informative to consider (figure 1 and table 1). These two kinds of 'individual selection' are not just two ways of looking at the same thing.

Our homogeneous group models show that in the absence of within-group selection (individual selection, meaning 1), one can still separate the effects of 'global' individual selection from group-specific selection (equation (4.1), figure 1 and table 1). Contextual analysis of a soft selection case shows that in the absence of group selection (meaning 1), one can still separate the effects of group selection (meaning 2) from the effects of within-group selection (individual selection, meaning 1) (table 1).

What about cases in which there is variation within the group and the Price partition results in two non-zero terms? Consider evolution in the two-locus modifier models described in appendix A. For these models, the Price equation partitions trait change into two non-zero terms. There are frequency changes of cell types within the development of the cell group (i.e. within-group individual selection) and frequency changes of cell groups based on group characteristics. Both levels are at play and both affect the frequency of cell types. The Price equation (issues related to pseudo-groups notwithstanding) captures the interplay of these two levels and may be used to understand the evolution of modifiers of development that affect the opportunities for both within- and between-group selection as discussed in appendix A.

Michod & Roze [49, p. 10] discuss the issue of pseudo-groups that comes up in their modifier models, showing how global individual selection is also an issue in these more traditional MLS models. Colonies with more D cells (cells that replicate faster, all else equal) would be fitter than those with fewer, even if the groups were not based on any interactions among cells. The high-replication-rate cells do better in competition within each proto-organism, and these are the same cells that (for the same reason) would do better without any group context at all. It would seem that global individual selection is not so distinct from within-group selection that it can act in an opposing direction (i.e. traits that are good in competition within a group would be good in competition without any group structure), so one may question what exactly the global-versus-within-group distinction means in the context of these models. Still, the distinction comes up in the conflict mediation models, particularly when group size can vary, indicating an area in which further exploration would be useful. Because global individual selection remains in the absence of within-group selection, the homogeneous group models show that the distinction cannot be entirely a matter of perspective.

Part of the debate surrounding partitioning levels of selection may come from the (usually implicit) assumption that two hierarchical levels of organization produce two potential kinds of selection (one corresponding to each level). It is important to keep distinct at least two meanings of group selection and two meanings of individual selection. Our modelling shows that they are distinct and important aspects of evolution in group-structured populations, particularly during an ETI. The fact that global individual selection can be modelled when within-group individual selection is zero means that there are at least three categories of selection that can be occurring together when there are two hierarchical levels of organization (figure 1).

6. Evolutionary transition in individuality progression and meanings and partitions of group and individual selection

Unicellular *Chlamydomonas reinhardtii* and multicellular *Volvox carteri* often serve as conceptual bookends or clear cases in which individuality applies unproblematically primarily at the cell level in the case of *C. reinhardtii* and primarily at the cell-group level in the case of *V. carteri*. But to understand the transition from one kind of case to the other, we must grapple with the questions of how to recognize and quantify progression through an ETI and the shifting notions of fitness that must occur as the transition proceeds. In broad strokes, authors often agree that ETIs are characterized by the process of natural selection taking hold at the group level and weakening at the lower level. These are not usually thought of as separate processes, but rather in terms of a change in a single trait (like allocation of resources to growth or investment in flagellar action) that has contrasting effects at the two levels. See Clarke [52] for more on the connection between quantifying levels of selection and characterizing ETI progression. There are two ways in which one can think about 'weakening' natural selection at the lower level, and these parallel the two meanings of 'individual selection' described in §5 (table 1).

One way in which natural selection can be said to take hold at the higher level and weaken at the lower level can be seen by shelving the issue of pseudo-groups and considering the standard Price multi-level partition (equation (2.3)). The evolution of factors that increase the between-group fitness–trait covariance and/or decrease the within-group fitness–trait covariance (equivalently, increase higher-level trait heritability) can be seen as promoting progression through the ETI. The fixation of the germline modifier in the Michod & Roze [49] model discussed in appendix A is an example. The life cycle modelled is such that cell groups develop from a single cell and then contribute propagules to a reproductive pool. There is a temporal phase of within-group cell-level selection followed by a phase of between-group selection (Okasha [4] mentions this temporal interpretation on p. 236). A central result of the modifier models was that after an ETI (after the modifier increased and the population shifted from the equilibrium without the modifier to one with, as discussed in appendix A), average cell fitness (meaning cell replication rate within the group during the 'development' phase) decreases while average group fitness increases. This result was derived and illustrated in different models and papers (see, for example, figs 12–14 of Michod & Roze [49], fig. 6-6 of Michod [13], fig. 2 of Michod [53], figs 9.1 and 9.2 of Michod [54]).

These results of weakening selection at the cell level and strengthening selection at the group level were described as the 'transfer of fitness' between the cell and group levels. The reason behind this description concerned the evolution of altruism, which played a special role with respect to a diachronic view of within-group versus between-group selection in the mathematical models referenced in the last paragraph. The costs of altruism decrease the within-group fitness of the lower-level units, while benefiting the fitness of the group, the higher-level unit. The relationship between the costs, C, and benefits, B, for altruism to evolve depends on relatedness as given by Hamilton's rule. In simplified form, Hamilton's rule says that C units of fitness may be subtracted from the cell level, as long as B units of fitness are added to members of the group. In this sense, the evolution of altruism transfers fitness from the level of the cell to the level of the group.

We see a strong connection between Clarke's [52] proposed framework for ETI progression and this first approach. Clarke [52] uses the Price partition to quantify levels of selection, and refers to 'individuating mechanisms', which are similar to conflict mediators such as germline modifiers discussed above and in appendix A. Our discussion so far in this section has shelved the issue of pseudo-groups. Clarke [52] works around the pseudo-group problem by defining groups in a particular way (related to individuating mechanisms). Our response to the pseudo-group problem does not involve parsing the definition of groups, but rather the causal effects that are specific to groups. A full comparison of the relative merits of these two 'solutions' to the pseudo-group problem is beyond our scope here and would be needed to make detailed comparisons between our ideas of ETI progression and those of Clarke [52].

The idea of global individual selection (meaning 2, table 1) can also be used to understand how lower-level natural selection may change as an ETI progresses. With reference to this meaning, progression through the transition can be seen when cells lose their capacity to function as independent wholes, instead becoming well-integrated parts of a larger whole. The decline in cell fitness for this meaning is counterfactual; the fitness a cell would have on its own declines as the transition progresses. This approach is described separately from the 'conflict mediator' approach because it relates to different models (i.e. homogeneous group models). We expect that further work would result in a more unified approach to the question of how MLS quantification relates to ETI progression.

In the homogeneous group models described above, group fitness is always the same as cell fitness by definition. This is shown mathematically in the appendix of Shelton & Michod [28], but is also intuitive given our assumption of small, clonally related groups. In spite of this group/cell fitness equivalence, there can still be the kind of increased integration and cohesion that we associate with ETI progression in these models. Cells become better at being parts of a whole and worse at being independent units because the value of their life history trait changes in response to being in a group. The counterfactual fitness, the fitness that they would have as unicells, declines as the evolutionary transition progresses in the model.

This unicellular or counterfactual meaning of 'cell fitness' also figures prominently in our reasoning about a set of life-history models of group integration through cell specialization, in which both the cell and colony level are characterized by investment in viability and fecundity (e.g. [53,55]). In this life-history optimization model, within-group selection is absent by assumption and selection is at the group level. The basic question addressed in this model is: under what conditions should the group contain cells that are specialized in one or both of the two components of fitness, viability and fecundity?

The meaning of 'cell fitness' in these models has been the subject of some commentary. Godfrey-Smith [56] and Bourrat [57] argue against the idea that actual cell fitness within a colony goes to zero at the end of the transition, a position that they attribute incorrectly to Michod [58].[7] In the modelling paper being described in Michod [58], Michod et al. [55, p. 263][8] state: 'Most important (and critical to our analysis) is the fact that, if one cell has a high fecundity (and hence a low viability, so that it would have a low fitness by itself), this may be compensated for if another cell has a high viability (and hence low fecundity). Consequently, even though each of these cells by itself would have a low fitness, together they can bring a high fitness to the group (especially under conditions of convexity of the trade-off)'. So, the idea in the model is clearly a counterfactual sense of 'cell fitness', the fitness a cell would have were it alone. Arguments against the idea that actual cell fitness in the group goes to zero (Godfrey-Smith [56], Bourrat [57]) are not relevant to the models (Michod [58], Michod et al. [55]) and do not inform our interpretation of them.[9]

In Michod et al. [55], an isomorphism was assumed between cell traits and colony traits, in the sense that if a cell (in a group) contributes v or b effort to viability or fecundity, respectively, then this same effort is also expended towards the respective group fitness components. Godfrey-Smith [56] either rejects or does not appreciate this early isophorphism and the counterfactual sense of 'cell fitness' used in the models. For example, Godfrey-Smith [56, p. 78] writes: 'Germline cells do not contribute to maintenance of viability. This functional contrast has to do with the cells' relations to the collective's fitness, not their own'. Michod et al. [55] provide a rationale for thinking that this isomorphism may hold early in an ETI in the volvocine alage.

Leslie et al. [59] also addressed the meaning of 'cell fitness' in Michod et al. [55]. The counterfactual meaning of 'cell fitness' is clearly articulated in Michod et al. [55] (see the above quote). Yet the trade-off between lower-level v and b is affected by the number of cells per colony (a higher-level trait), so the 'cell-level' fitness components do have a connection to the group and are not just the fitness a cell would have by itself. Leslie et al. [59] offer a possible solution to this concern. A full exploration of the issue is beyond our scope here.

7. Conclusion

Clarity concerning fundamental evolutionary concepts such as fitness and selection is needed to better understand the 'shifting ground' that is characteristic of evolutionary transitions individuality. The single-level Price equation maps to commonly accepted 'conditions' for natural selection, and so it is closely linked to the fundamental concept of selection. Beginning with Lewontin [2] and Maynard Smith [3], it was assumed that the conditions for natural selection were sufficient for understanding the occurrence of natural selection. The straightforward multi-level expansion of the Price equation was a promising approach to quantifying selection at different levels, indeed Hamilton [24] referred to it as a formal separation of levels of selection. However, the problem of pseudo-groups calls this partition, along with the conditions approach upon which it is based, into serious question as a sufficient framework for understanding selection in group-structured populations. It is now clear that there is more to the problem of MLS than the conditions approach alone can resolve, and explicit mathematical models are needed to clarify causation of selection in group-structured populations. We describe how consideration of group selection models motivated by the volvocine green algae helps clarify different meanings of group and individual selection (table 1 and figure 1). We develop a counterfactual approach to partitioning group and individual selection. This approach contrasts counterfactual fitness, the fitness a cell would have were it outside the group, with the actual fitness attained when part of a group. An assumption of this approach is that only group selection can make cells suboptimal when the cells are removed from the group (stochastic effects and similar complications aside), so this approach should help us pinpoint 'group selection'. We develop a partition of group and individual selection, equation (4.1) (figure 1), that correctly attributes the degree of group and individual selection in problem cases like when there are pseudo-groups. Unlike the Price approach, the counterfactual approach has the feature that the degree of group-specific selection increases continuously with the degree of group effect. Furthermore, as the ETI proceeds, group fitness becomes decoupled from counterfactual fitness. We find that when there are two levels of selection, there are at least three kinds of selection that need to be distinguished and can be occurring together in a group-structured population: group-specific fitness, within-group individual fitness and global individual fitness. Analysis of concrete cases like the volvocine green algae, along with partitions of selection based on explicit mathematical models, are instructive for determining the underlying causes of selection in group-structured populations. We agree with Sober [46, p. 230] and think our analysis is in line with his recommendation: 'When group and individual selection both affect the evolution of a trait, is there a uniquely correct answer to the question of how strong each cause is? It is pointless to speculate about this in the abstract. We need to get down to details concerning how a causal partition might be effected'.

Data accessibility. This article has no additional data.

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Appendix A. Evolution of conflict mediation during an ETI and the Price equation

In this appendix, we review an application of the Price equation to theoretical work on conflict mediation during an ETI. Michod and Roze [13,47–51] developed explicit two-locus population genetics models for the unicellularity-to-multicellularity ETI involving both within-group and between-group variation and change. The models show that cooperation among cells in a proto-organism is vulnerable because traits that benefit the cell and harm the cell group can thrive within each cell group. This is similar to issues that have been much discussed in a synchronic context. The diachronic context in these models comes from consideration of the evolution of modifier traits, traits such as a germline or programmed cell death. Modifier traits are assumed to affect development of the multicellular group and can tip the balance in favour of cooperation by changing aspects of development that affect the interplay of levels of selection. By subverting within-group natural selection, modifiers can set the stage for enhanced cooperation and elaborate integration of cell groups into adaptive wholes. The recursion equations describing the dynamics of both cooperation and modifier alleles do not draw on the Price equation. The Price equation partition was used to help show what is happening during the spread of the modifier in terms of levels of selection.

Michod & Roze [49] consider several variants of a two-locus modifier model. Here, we describe the model in Michod & Roze [49]; see §§3–6 with the germline modifier from §4.5. This model is also described and discussed in Michod [13]; relevant pages are referenced here. The model is of a life cycle that alternates between haploid and diploid with the haploid stage being multicellular.[10] A cell group (i.e. proto-organism) begins as a single haploid cell which then undergoes rounds of cell division. Haploid cells are characterized by two loci, each having two alleles. The first locus determines if a cell is a cooperator (`C`) or defector (`D`), explained further below. The cell group grows via cell division, with `C` and `D` cells having different replication rates. Cells with the `D` allele 'defect' by not contributing to group-level functioning and thereby increase their own reproductive rate relative to `C`-allele cells. The larger, adult cell group then emits haploid gametes according to its final size and composition. All else equal, a group with a higher proportion of `C` cells will produce more gametes because the `C` cells contribute to the group's functionality. Gametes then fuse and the resulting cell undergoes meiosis, completing the life cycle [13, p. 110]. In this model, cells occasionally mutate from `C` to `D` (but not `D` to `C` because gain-of-function mutations are assumed rare enough to ignore). The second locus modifies the life cycle and how the groups develop, and thus selection on the first locus. An example of a modifier trait is the early sequestration of a germline. For this germline modifier, cells with the m allele (no modifier) make gametes using all the cells from the adult group. Cells with the M allele (with the modifier) make gametes from a cell line that has undergone fewer divisions than the rest of the cell group (i.e. from a sequestered germline). Other modifiers considered by this approach include mutation rate, self-policing and fixed adult size [13, pp. 113–122; 60].

For this population genetics model of MLS at two loci, three of the four possible equilibria are biologically relevant:[11] equilibrium 1 has only Dm cells, equilibrium 3 has Cm and Dm cells, and equilibrium 4 has CM and DM cells [13, p. 114]. Equilibrium 1 occurs when the advantage of defection is high. In this model, within-group selection favours defector (D) cells and between-group selection favours cooperator (C) cells. Thus, for there to be a population that is polymorphic for C and D (equilibriums 3 and 4), selection at the two levels must be in balance. This balance means that the first and second term on the r.h.s. of the Price equation (equation (2.2)) are equal in magnitude. In equilibrium 3, the population is fixed for no germline modifier (m). The C/D polymorphism consists of cooperating cells being maintained at relatively low frequencies [13, p. 123 and fig. 6–3]. The exact level of cooperation depends on several parameter values, but the general observation of low cooperation in a population fixed for m holds. For a population in equilibrium 4, again cell- and group-level selection are in balance. However, the frequency of the cooperator (C) allele in this equilibrium can be dramatically higher.

Michod [13, p. 124] uses the Price equation to illuminate what happens during a transition from equilibrium 3 to equilibrium 4. As the M allele goes from low frequency to becoming fixed, the two levels of selection are not in balance. The magnitude of selection between groups, $\mathrm{Cov}_i(w_i,z_i)=w$, exceeds the magnitude of within-group change, $E_i[w_i D z_i]=w$. Additionally, the new balance that is achieved when M becomes fixed occurs at lower values for both terms. Recall that the $E_i[w_i D z_i]=w$ term includes the effect of lower-level selection, which can be seen as 'property change' at the higher level. Since the levels of property change are lower in equilibrium 4 compared with equilibrium 3, the population has evolved to have higher heritability of traits (and therefore higher heritable fitness) at the group level.

This model takes a decidedly diachronic view on levels-of-selection questions. It is not enough to know which levels are at play in a given scenario. ETIs raise the questions of how the higher level emerged in the first place and how the higher level can gain in its capacity to evolve by natural selection. The two-locus modifier models suggest a way in which features of the higher-level reproductive system can themselves evolve by group selection, and the Price equation analysis helps to highlight the within-group versus between-group selective dynamics.

Endnotes

[1] See Lewontin [2], Maynard Smith [3] and Okasha [4] for more discussion on natural selection conditions.

[2] See Goodnight [37] for an explanation of the idea that soft selection should be seen as a case of group selection (i.e. that group selection is counteracting individual selection to equalize fitness among the groups).

[3] Another example of using fitness-affecting interactions to define groups is given by Uyenoyama & Feldmen [44], who write: 'A group is the smallest collection of individuals within a population defined such that genotypic fitness calculated within each group is not a (frequency-dependent) function of the composition of any other group'. See also Michod [45].

[4] Another consequence of the biology of these organisms is that unambiguous spatio-temporal groups of cells exist, so it is relatively unambiguous to decide what the potential 'group' is.

[5] There is a minor notational difference. In Shelton & Michod [28], we worked in terms of relative fitnesses, whereas here we present things in terms of absolute fitnesses.

[6] For this model, one can call it the group effect on group fitness or the group effect on individual fitness; that distinction is a matter of perspective only.

[7] Godfrey-Smith [56] does acknowledge, in reference to a point about both cell types actually surviving and dividing within a group, that Michod 'does not intend to deny any [of] those assertions about what germline and somatic cells do'.

[8] The modelling paper described in Michod [58] was referred to as 'Michod et al. 2005. In Press'. However, this paper ended up being published in 2006 [55].

[9] The confusion in the Godfrey-Smith [56] and Bourrat [57] papers appears to partly stem from Michod [58] not using the subjunctive (the fitness cells would have were they alone), when that was the idea based on the construction of the model. Michod [58] also writes: 'Therefore, the fitness of the group is zero under MLS1, yet group fitness may be quite high under MLS2'. This could be an additional source of confusion because 'MLS1 group fitness' does not typically mean the average of counterfactual fitnesses (average of the fitnesses that the constituent cells would have had as unicells).

[10] Having the multicellular stage be haploid is simply for convenience and does not bear on the results and conclusions.

[11] Equilibrium 2 has only DM cells and is not biologically relevant.

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