CORRESPONDENCE

More on the genetical theory of multilevel selection

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Abstract

In my article *The genetical theory of multilevel selection*, I provided a synthesis of the theory of multilevel selection (MLS) and the theory of natural selection in class-structured populations. I framed this synthesis within Fisher's genetical paradigm, taking a strictly genetical approach to traits and fitness. I showed that this resolves a number of long-standing conceptual problems that have plagued the MLS literature, including the issues of 'aggregate' vs. 'emergent' group traits, 'collective fitness$_1$' vs. 'collective fitness$_2$' and 'MLS1' vs. 'MLS2 '. In his commentary, Goodnight suggests this theoretical and conceptual synthesis is flawed in several respects. Here, I show this is incorrect, by: reiterating the theoretical and conceptual goals of my synthesis; clarifying that my genetical approach to traits is necessary for a proper analysis of the action of MLS independently of non-Darwinian factors; emphasizing that the Price–Hamilton approach to MLS provides a consistent, useful and conceptually superior theoretical framework; and explaining the role of reproductive value in the study of natural selection in class-structured populations. I also show that Goodnight's contextual analysis treatment of MLS in a class-structured population is mathematically, biologically and conceptually inadequate.

Introduction

In my article *The genetical theory of multilevel selection* (Gardner, 2015), I provided a synthesis of the theory of multilevel selection (MLS) and the theory of natural selection in class-structured populations. I framed this synthesis within Fisher's (1918, 1930, 1941) genetical paradigm, taking a strictly genetical approach to traits and fitness. I showed that this resolves a number of long-standing conceptual problems that have plagued the MLS literature, including the issues of 'aggregate' vs. 'emergent' group traits, 'collective fitness$_1$' vs. 'collective fitness$_2$' and 'MLS1' vs. 'MLS2' (reviewed by Okasha, 2006).

Goodnight (2015) suggests this theoretical and conceptual synthesis is flawed in several respects. He suggests that I did not adequately review the empirical literature on MLS, that I employed a flawed definition of evolutionary traits, that I framed my contribution within a flawed Price–Hamilton tradition and that I did

not correctly describe MLS in the context of class-structured populations.

Here, I: (1) reiterate the theoretical and conceptual goals of my synthesis; (2) clarify that my genetical approach to traits is necessary for a proper analysis of the action of MLS independently of non-Darwinian factors; (3) emphasize that the Price–Hamilton approach to MLS provides a consistent, useful and conceptually superior theoretical framework; and (4) explain the role of reproductive value in the study of natural selection in class-structured populations. I also (5) show that Goodnight's contextual analysis treatment of MLS in a class-structured population is mathematically, biologically and conceptually inadequate.

Evidences of multilevel selection

Goodnight suggests that I did not satisfactorily review the empirical literature on MLS, and he provides a brief overview to remedy this perceived oversight. However, the empirical reality of various evolutionary phenomena that researchers have referred to as MLS is not in dispute here. The real issue is that MLS researchers have been unable to agree upon exactly what MLS and

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its associated concepts actually mean, and it is this issue that provided the motivation for my theoretically and conceptually focused synthesis. I made this clear in the opening sentences of the Abstract:

> The theory of multilevel selection (MLS) is beset with conceptual difficulties. Although it is widely agreed that covariance between group trait and group fitness may arise in the natural world and drive a response to 'group selection', ambiguity exists over the precise meaning of group trait and group fitness and as to whether group selection should be defined according to changes in frequencies of different types of individual or different types of group.

Nevertheless, Goodnight's empirical overview does helpfully illustrate the muddle of definitions that are being used in the study of MLS. Importantly, whereas many of the studies that he mentions define group selection in terms of the proliferation and/or extinction of groups (e.g. Pruitt & Goodnight, 2014), others define group selection in terms of the impact that an individual's group environment has on her own fitness (e.g. Stevens *et al.*, 1995). These definitions are not equivalent, and will often disagree with each other as to the existence, magnitude and direction of group selection in particular scenarios (more on this, below).

I do disagree with Goodnight when he suggests that these empirical studies have vindicated the 'old' group selectionism of Wynne-Edwards (1962). It is true that artificially imposed, industrial batch-level selection in poultry may lead to increases in yield (Muir, 1996), but this is a world away from Wynne-Edwards' claim that whenever selection acting within wild populations is in opposition to selection acting at the between-population level, it is the latter that must prevail such that adaptation in the natural world is always 'for the good of the group' (Wynne-Edwards, 1962, p20). Both of these points serve to illustrate the conceptual confusions that abound in the MLS literature.

Multilevel selection is not evolution

Goodnight suggests that my theoretical synthesis is flawed on account of my conception of evolutionary traits being defined only for well-mixed populations. This is incorrect. The definition that I used is valid, conventional and appropriate to the aims of my study. My impression is that this confusion has arisen out of MLS being conflated with total evolutionary change.

Here is how I introduced the genetical approach to traits:

> The character under selection is the heritable portion of the individual's phenotypic trait, *g*; that is, a weighted sum of the frequencies of the alleles that the individual carries, the weights being decided by linear

regression analysis... This quantity is also known as the individual's 'breeding value'

This linear regression approach to describing the genetical component of the phenotype was introduced by Fisher (1918), and it is conventionally termed 'breeding value' (Falconer, 1981, pp106–107). The application of breeding values within the context of Price's equation was spelled out by Price (1970), and they are clearly defined even for populations that are not well mixed (Falconer, 1985). Indeed, it is the variance in breeding value that actually defines the 'additive genetic variance' (Falconer, 1985) that is central to Goodnight's own approach to MLS in structured populations (see below). If breeding value were really undefined except for in well-mixed populations, then the same would be true of additive genetic variance.

Goodnight's concern with the breeding value approach seems to be that the regression terms depend upon context. A gene's average effect with regard to a phenotype of interest may depend on its interactions with other genes and with factors like climate such that, in subsequent generations, when the gene may find itself incorporated into different genotypes and experiencing different climates, its average effect is liable to change. Consequently, the same genotype is liable to have different breeding values in different generations.

It is true that such changes in breeding value are not explicitly represented in my equations. However, they are allowed for, in the sense that the equations remain valid irrespective of such changes occurring. The reason that they do not feature in the equations is that my explicit aim was to describe only the action of natural selection, and these changes in breeding value are not part of natural selection, but instead represent a distinctly non-Darwinian factor in evolution. In the context of Price's (1970, 1972a) theorem, such changes accrue to the 'transmission' term. In the context of Fisher's fundamental theorem, such changes contribute to 'deterioration of the environment' (Fisher, 1930, p41, 1941; Price, 1972b). I discussed both transmission and environmental deterioration as part of the explication of my theoretical synthesis, making clear that these are conceptually distinct from the action of MLS.

The careful separation of selection and transmission effects is not merely a matter of convention, but actually necessary from an adaptationist standpoint. It is only natural selection, and not transmission factors – such as spontaneous random mutation and fluctuating average effects – that gives rise to adaptive design (e.g. Gardner, 2009; Gardner & Welch, 2011). It is this unique role of natural selection that motivated the focus of Fisher's (1930) *The genetical theory of natural selection*, and his opening sentence: 'Natural Selection is not Evolution'. Fisher's fundamental contributions to Darwinian theory, and the contributions of others who

have worked within his genetical framework, will continue to be misunderstood for as long as the concepts of natural selection and evolution are conflated.

Multilevel selection and covariance

Goodnight suggests my theoretical synthesis is also flawed on account of it being framed within the Price–Hamilton approach to MLS (Price, 1972a; Hamilton, 1975). In particular, he points out that the Price–Hamilton formalism may detect the operation of group selection even for nonsocial behaviours, and he suggests that an alternative, contextual analysis approach provides the correct means of capturing the action of MLS. I believe that both the Price–Hamilton and contextual analysis approaches yield useful insights, but that it is the former rather than the latter that properly engages with the ideas of selection and adaptation at the group level. Moreover, I believe it is desirable – rather than problematic – that the Price–Hamilton approach is able to diagnose the operation of group selection beyond the realm of social behaviour.

Price's (1970, 1972a) selection–covariance theorem provides a very general framework for thinking about selection in any context and in any medium. In the context of evolutionary biology, it defines the action of natural selection in terms of a partial change in the average value of a genetical trait, and it reveals that this change is equal to the covariance, taken across all the individuals in the population, between the individual's genetical trait and her relative fitness. It is intuitive, then, that group selection should be defined analogously, as the covariance, taken across all the groups in the population, between the group's genetical trait and the group's fitness. This is exactly the Price–Hamilton approach to MLS. This approach conceives of the group itself as the unit of group selection, it assigns the group its own fitness, and it views group selection as being driven by the differential fitness of groups *per se*. Importantly, by focusing on the group's fitness, it directly connects with ideas of adaptation 'for the good of the group'.

In contrast, although contextual analysis is also rooted in Price's covariance definition of natural selection, it instead conceives of group selection in terms of the impact that the individual's social environment has on the individual's fitness. Accordingly, it conceptualizes the individual as the unit of group selection, and it views group selection as being driven by the differential fitness of individuals *per se*, rather than the differential fitness of groups. This is how contextual analysis is able to diagnose the action of group selection in the context of soft selection, for example, despite all groups having equal fitness. Put another way: whereas the Price–Hamilton approach isolates the part of natural selection that corresponds with the adaptation of groups, contextual analysis isolates the part of natural selection that

corresponds with the adaptation of individuals to their particular group contexts. Both are useful approaches for studying selection, but only one appears to be properly engaging with the concept of group selection.

It is true that the Price–Hamilton approach may diagnose the operation of group selection in some scenarios that do not involve social behaviour. For example, if some individuals have better eyesight, and if some groups – by chance – have more better-sighted individuals than others, then a portion of the action of natural selection for improved eyesight will occur at the between-group level. However, although this point has been much discussed in the literature for the last ~30 years, there does not appear to be any consensus on whether it is actually fatal to the Price–Hamilton approach.

My own view is that, far from being fatal, this diagnosis of group selection beyond the realm of social behaviour is actually desirable (Gardner & Grafen, 2009). The MLS partition of natural selection into its within-group and between-group components is not supposed to delineate the boundary between the social and nonsocial realms: that is the job of the kin-selection partition of natural selection into its direct-fitness and indirect-fitness effects (Hamilton, 1964, 1970; Gardner *et al.*, 2011). Moreover, it would be a mistake to view within-group selection as the sole driver of individual-level adaptations, including good eyesight; rather, it is the total action of natural selection, acting both within and between groups, that leads individuals to become adapted to maximize their inclusive fitness (Gardner & Grafen, 2009). Instead, the conceptual significance of the MLS partition is that it separates natural selection into the component that is responsible for group-level adaptation (i.e. between-group selection) and the component that acts to undermine the adaptive integrity of groups (i.e. within-group selection; Gardner & Grafen, 2009).

If natural selection is acting – wholly or partially – at the within-group level, then traits will not be favoured to maximize group fitness and any adaptive rationale will need to be sought at a lower level. But if natural selection is acting only at the between-group level – for example if groupmates are genetically identical clones – then adaptations will evolve for the good of the group (Gardner & Grafen, 2009). Note that, in scenarios permitting a group-adaptationist interpretation, one is free to interpret a trait like good eyesight either as an individual-level adaptation for maximizing the individual's inclusive fitness or a group-level adaptation for maximizing the group's inclusive fitness. This is analogous to how one can view a macrophage engulfing a bacterium as either a cell maximizing its own inclusive fitness or part of a larger suite of adaptations employed by a multicellular animal for maximizing her inclusive fitness (Gardner, 2014). Adaptationism is a scientific tool that uses optimization thinking to formulate

testable predictions (Parker & Maynard Smith, 1990) and, in those special circumstances in which the interests of individual and group are aligned, it is empirically vacuous to debate whether it is the individual or the group that has been optimized.

Multilevel selection in class-structured populations

Turning to the specific issue of class structure, Goodnight suggests my approach to MLS in this context is flawed on both conceptual and technical grounds. In particular, he suggests that I have erroneously assigned fitness to only one level of biological organization – the individual – and he provides a contextual analysis treatment of MLS in haplodiploid parasitoid wasps that he claims is superior to my Price–Hamilton approach. Here, I suggest there has been a misunderstanding of the concept of reproductive value and its role in theory of natural selection, and I show that the contextual analysis treatment is mathematically, biologically and conceptually invalid as an alternative to the Price–Hamilton approach.

The concept of reproductive value is of crucial importance in the context of class-structured populations. If individuals differ in ways that are not strictly genetical, then they cannot be considered equivalent from a natural-selection perspective and must be subdivided into separate classes. One aspect of the problem of class structure is that not all offspring are equal, such that a simple count of offspring number may not provide an adequate measure of an individual's Darwinian success. A vivid example is provided by sex allocation, in which parents decide the sex, rather than the number, of their offspring (Darwin, 1871, p316; Fisher, 1930, pp141–143). Accordingly, a proper measure of Darwinian success is provided by the individual's reproductive value-that is, her expected, asymptotic, relative contribution of genes to future generations – and each class of individual contributes to the overall action of natural selection in proportion to its reproductive value (Fisher, 1930, p27). Taylor (1996) provides an introductory-level overview of the mathematics of reproductive value.

As an illustrative application of my theoretical and conceptual synthesis, I discussed the relationship between nontransmissible cancer and MLS. Although cancer has often been conceptualized as involving a tension between different levels of selection – that is, favoured at a within-individual level and disfavoured at a between-individual level – I pointed out that the proliferation of cancer cells cannot be conceptualized in terms of MLS, in the strict sense of the genetical theory, because cancer cells – and somatic cells in general – have no reproductive value. But Goodnight suggests that my logic is faulty: he argues that as cancerous cells have the capacity to proliferate and exhibit heredity,

their proliferation does represent within-individual selection, and that my conclusion had stemmed from an erroneous assignment of fitness only at the level of individual organisms.

However, this is incorrect: I did not assign zero reproductive value to cancer cells because they are cells and not individuals, but rather because they are cells whose lineages perish with the death of the individual organism, such that their expected, asymptotic, relative contribution of genes to future generations is zero. Even if reproductive value is assigned only to cells and not to whole organisms, all of the reproductive value in the population belongs to germ line cells, whereas somatic cells have zero reproductive value. Thus, according to Fisher's proportionality principle, the proliferation of cancerous cells within somatic tissues cannot be part of MLS, in the strict sense of the genetical theory. (Of course, as cancer may induce differential reproductive value of germ line cells, at a between-organism level, it may lead to the selective favouring of anticancer adaptations).

The role of reproductive value in modulating a class's contribution to the overall action of natural selection is captured mathematically by Price's (1970) equation for class-structured populations – specifically, Price's equation (5) and my equation (4). This describes a separate selection covariance for each class in the population and adds them together to yield the total action of natural selection, with each class's contribution being weighted by its reproductive value (such that a class with no reproductive value makes no contribution at all). As part of my theoretical synthesis, I combined this equation with Price's (1972a) equation for MLS – specifically, Price's equation (A17) and my equation (5). This provided a statement of MLS for class-structured populations – specifically, my equation (7). This equation takes each class's separate contribution to the total action of natural selection and separates its within-group and between-group components, such that the total action of group selection is defined as a class-reproductive-value-weighted sum of the between-group selection terms for each class.

In my study, I pointed out that this formulation presents some conceptual problems for the idea of the social group as a unit of selection. In particular, although in some scenarios the sum of between-group selection terms can be brought together as a single selection covariance, with the social group acting as a unit of selection, more generally the social group remains fragmented into its separate pure-class subgroups, and it is these that are considered the units of group selection, rather than the whole social group. To illustrate the problem, I considered the following scenario:

> For example, a parasitoid wasp might oviposit a single unfertilized (i.e. male) egg and a single fertilized (i.e.

female) egg into a caterpillar, within which these siblings develop and compete for resources, and this yields both a clearly defined social group of more than one individual and also ample scope for kin selection. Yet, it is unclear whether group selection can occur, except in the trivial sense that a single individual can be considered a group of size 1, owing to difficulties in bringing the separate selection covariances for male subgroups and for female subgroups together into a single selection covariance.

Goodnight suggests that this Price–Hamilton approach is simply flawed and instead provides a treatment of this parasitoid wasp scenario using his preferred contextual analysis approach. He states that the response to selection for arbitrary individual-level and group-level traits is given by $R = \frac{1}{2}\ (G\ P_F^{-1}\ S_F + G\ P_M^{-1}\ S_M)$, where P_F and P_M are 3×3 phenotypic covariance matrices describing female, male and group traits in females and males, respectively; G is the corresponding 3×3 genetic covariance matrix; and S_F and S_M are vectors of order 3 describing the selection differentials in females and males, respectively. This is a modified version of Lande's (1980) classic result.

However, this contextual analysis treatment is problematic in several respects. Firstly, it is mathematically invalid because the phenotypic covariance matrices, being singular, are uninvertable, so the right-hand side of the equation is actually undefined: this is the linear algebraic equivalent of a division-by-zero error. To be clear, this error is present only in Goodnight's treatment, and not in Lande's formulation. Secondly, the contextual analysis treatment is biologically invalid because it implicitly assumes a diploid mode of inheritance, which is incompatible with the haplodiploid mode of inheritance exhibited by parasitoid wasps (both in reality and in the hypothetical scenario outlined above). Lande's article does contain a result for haplodiploidy, in the Appendix, that might serve as the basis for a reworked contextual analysis treatment. Thirdly, the contextual analysis treatment hinges upon particular, ad hoc assumptions – such as Gaussian variance, made explicitly by Lande but left implicit by Goodnight – that may yield a more or less reasonable approximation in the context of particular applications, but which fundamentally limit its wider generality. This contrasts with the Price–Hamilton approach to MLS, which emerges from notational definitions as an exact mathematical identity, and thereby enjoys much fuller generality of mathematical and empirical application.

Acknowledgments

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