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From Fitness-Centered to Trait-Centered Explanations: What Evolutionary Transitions in Individuality Teach Us About Fitness

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Abstract

Fitness has taken center stage in debates concerning how best to identify evolutionary transitions in individuality (ETIs). An influential framework proposes that an ETI occurs only when fitness is exported from constituent particles to a collective. We reformulate the conceptual structure of this framework as involving three steps. The culminating step compares “counterfactual” fitnesses against a long-run measure of fitness. This comparison assumes that collective-level fitness mereologically supervenes on particle fitness. However, if this assumption is rigorously enforced, the proposed conditions for identifying ETIs prove to be too weak. We here suggest an alternative model of ETIs centered around traits.

1. Introduction

An evolutionary transition in individuality (ETI) is thought to have occurred when the fitness-affecting interactions among individuals at a lower level of organization are structured in a way that subsequently maintains the minimal organizational requirements of a would-be individual on a higher level. That such transitions have occurred is beyond doubt (Bourke 2011; Maynard Smith and Szathmáry 1995; Michod 2005; Okasha 2006). Chromosomes evolved from their constituent genes. Eukaryotic cells evolved from ancestral prokaryotic cells. The evolution of complex multicellular eukaryotes began with simpler single-celled precursors. Nearly universal agreement among biologists on the fact that such transitions occurred can nevertheless obscure the fact that we still know relatively little about *how* or *why* ETIs occur. Insight into what general mechanisms and evolutionary dynamics might explain the phenomenon remains elusive despite more than half a century of exploration into ETIs.

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There have, however, been some promising moves in the direction of identifying desiderata that any set of definitional conditions for an ETI must heed. Among the most intriguing is the proposal that an ETI cannot take place unless the fitnesses of constituent organisms on a lower level are somehow “transferred to” the fitness of a newly established (higher-level) individual composed by them. For simplicity, we herein refer to this view as the “fitness-transfer framework.” Despite its promise as a potential indicator for the presence of ETIs (section 2), we argue that this framework suffers drawbacks that limit its utility as a causal explanation of ETIs (section 3). In its stead, we advocate (section 4) for an approach to identifying ETIs that emphasizes the mechanistic decomposition of fitness into traits (e.g., vital demographic rates) whose interrelationships (trade-offs and subsequent escape from them) help further elucidate ETIs.

2. The prevailing view: Fitness-transfer

When it comes to determining whether ETIs have occurred, the orthodox view is arguably one couched squarely in terms of interlevel “fitness transfers” (Michod 2005; Okasha 2006; Folse and Roughgarden 2010; Shelton and Michod 2014, 2020). Explaining this approach with the minimum amount of mathematical formalism requires abstracting away from the specificities of examples like those noted in the preceding text. We subsequently refer to individuals on a lower level of biological organization as “particles,” while retaining the term “collective” for the aggregation of lower-level individuals within a higher-level entity. For readers who prefer a slightly more concrete case, the evolution of multicellularity from ancestral single-celled organisms works well as a stand-in for our maximally abstracted scenario. The guiding intuition behind the fitness-transfer framework is that ETIs have occurred whenever the fitness of a collective becomes “decoupled from” the fitness of its constituent particles. When such a distinctive pattern of decoupling is observed, it is argued that a (causal) process of particle-level fitness “transfer” or “export” to the collective must have occurred. Only upon the conclusion of this process could the resulting collective subsequently become an (evolutionary) individual.

Before presenting the conceptual backbone of this framework, a preliminary remark is needed to situate it within evolutionary theory more broadly. One of the main problems for the emergence of cooperation, of which collective-level individuality is an instance, is the free-rider problem. Speaking very generally, a “free rider” is an individual who receives the benefit of a social good without contributing toward the cost of producing it. In the context of ETIs, the free-rider problem shows how the optimization of collective fitness (a presumed common good) is constantly jeopardized by the incentive that constituent particles (e.g., a gene) have to withhold contributing to it. In response to this, some have posited the need for so-called policing mechanisms (Clarke 2013) or conflict mediators (Michod *et al.* 2003) that would prevent the demise of primordial collectives due to free-riding. According to Michod and collaborators, “transfer of fitness from lower to higher-levels occurs through the evolution of cooperation and mediators of conflict that restrict the opportunity for within-group change and enhance the opportunity for between-group change” (*ibid.*, 96).

The fitness-transfer framework rests on an appealing metaphor. This heuristic must be unpacked if the aim is explanation. The notion of fitness features centrally because an alleged “transfer” of fitness is proposed as the fundamental criterion for

an ETI. The measure of fitness that most, if not all, parties to the discussion of ETIs have in mind is the asymptotic exponential long-term growth rate, or the so-called Malthusian parameter (Takacs and Bourrat 2022). The philosophical complications and mathematical technicalities associated with this measure need not presently detain us. Of importance here is the conceptual structure of a suggested method for identifying ETIs *given that there is an agreed-upon measure of fitness*.

The fitness-transfer framework's proposed methodology for identifying ETIs can be reconstructed as including just three pivotal steps (following Bourrat 2021, Figure 5). The first step measures the fitness of particle collections that have the potential to be collective-level individuals. This measure ("f3" or "F" in Bourrat et al. 2022) must be taken over a period much longer than a single-particle generation to correspond with a putative collective-level generation. What the fitness-transfer framework rightly demands are principled reasons to discriminate collective-level individuals from mere aggregations. The duration of time over which collectives persist, grow, and reproduce is given conceptual precedence because it determines the appropriate time frame for the measurement of particle-level fitnesses and thereby allows for such discrimination. Importantly, average particle-level fitness cannot differ from collective fitness in the long run; only the proposed allocation of fitness to one level or another can.

The components of collective-level fitness (probabilities of persistence, growth, and reproduction) are exhaustively characterized by the number of particles they contain and the interactions among those particles. Collectives increase in size ("grow") when their constituent particles reproduce and decrease in size ("shrink") when particles die. If constituent particles neither die nor reproduce, the size of the collective remains the same and it can justifiably be said to "persist" or "survive." Finally, collectives may "reproduce" when their particles (e.g., propagules) migrate to found new collectives. Growth, survival or persistence, and reproduction together are taken to be the most basic set of proxies for fitness in evolutionary biology and crucially function as the basis for fundamental life-history trade-offs (Stearns 1992). Insofar as these proxies can be fully characterized for a collective by reference to nothing more than the density and population dynamics of constituent particles, it can be argued that collective-level fitness mereologically *supervenes* on particle-level fitness.¹ This metaphysical relationship provides the groundwork for explaining ETIs because there is nothing more to collective-level fitness variation than variation in average particle-level fitness. However, as we shall see, some interpretations of the fitness-transfer framework have the worrying implication that this grounding assumption must be denied.

The second step of the fitness-transfer framework compels us to measure particle-level fitnesses *counterfactually*. Two distinct implementations of counterfactuality are possible. The first pertains to what particle fitness would be in an immortal collective that grows indefinitely without reproduction. This corresponds to particle fitness as measured within a collective (measure "f1" in Bourrat et al. 2022), which parallels the measure of individual fitness in trait-group models of multilevel selection (see Okasha 2006) that argue for group selection and the evolution of altruism. It provides a value of particle-level fitness that optimizes collective-level persistence.

¹ Okasha (2006, 106–107) seems to disagree with this picture. However, for lack of space, we cannot discuss his view on the matter or our response to it.

An alternative implementation of counterfactuality concerns prospective particle fitness in a state like that experienced by free-living ancestors (measure “f2” in *ibid.*). It thus considers the possibility that an observed particle has no direct or indirect interaction with other particles in a collective. Collectives are usually identified as interesting for the study of ETIs because we suspect that their persistence must be due to particle-particle interactions. In subsequent discussion of this second step, we rely only on this latter implementation of counterfactuality due to its direct connection to the measurement of particle fitness in some experimental settings. Further, it conforms more closely to the way that proponents of the fitness-transfer framework have recently discussed their approach (e.g., Shelton and Michod 2014, 2020). To obtain counterfactual measures of particle fitness, those who study ETIs as per the fitness-transfer framework must find a way to disentangle observed particle growth rates in a collective from the growth rates that would have been exhibited were there no collective-dependent effects (i.e., population structure). This can be done by introducing a selective regime that disrupts any existing population structure. In a laboratory setting, for example, this might be accomplished by physically agitating single-celled, colonial organisms such as bacteria in the *Pseudomonas* genus (Hammerschmidt *et al.* 2014). There are well-known advantages to forming microbial mats that prevent sinkage in liquid microcosms (e.g., nutrient-filled beakers). Centrifugal swirling and vibration can make prolonged mat-formation nigh impossible. Experimenters subsequently measure the evolution of particle-level growth rates in the wake of such periodic or prolonged perturbation. This regime eliminates any existing population structure and, thereby, any long-term advantages that would accrue to variants with increased proclivity toward mat-formation. It creates an experimental setting in which competition among variants reduces to the short-term competition between the strains, as would likely have been the case in an ancestral situation. Particles with higher short-term growth rates are predicted to dominate under this selective regime. A short-term measure of growth rates in this experimental setting could yield an estimate of what theoreticians call maximal growth rate during the initial phase(s) of exponential population increase.

The all-important final step of the fitness-transfer framework requires comparing the measured value of particle-level fitness over a long period involving events of collective-level reproduction (step 1) against the value of particle-level fitness attained from a counterfactual situation (step 2). A genuine ETI cannot, according to the fitness-transfer framework, occur unless there is a discrepancy between these two measures. Further, the counterfactual fitness of particles within a collective must be lower than the measure of particle fitness over the long term. Metaphorically speaking, this difference in value represents the “sacrifice” (in terms of growth rate) that particles make to ensure collective-level persistence. It is the totality of this fitness cost that can be potentially “transferred” or “exported” to a collective. If no discrepancy is observed, then the collection hypothetically posited as a higher-level (Darwinian) individual is nothing more than a mere collection or aggregation of particles.

3. Problems for the prevailing view

It is undeniable that the fitness-transfer framework has advanced the study of ETIs. Nevertheless, it confronts difficulties that cause us to question its adequacy. Our

overarching belief is that these difficulties stem directly from its reliance on the figurative idea of fitness transfer. This suggestive metaphor has taken on a life of its own in the work of those (e.g., Okasha 2006) who endorse a literal interpretation of the multilevel selection 1/multilevel selection 2 distinction, as initially proposed by Damuth and Heisler (1988).² Fitness is accordingly understood as an objectively measurable (mind-independent) and transferrable commodity (Doulcier et al. 2022). No longer is fitness “export” or “transfer” just the primary *indicator* of ETIs; it is now apparently also the *cause* of an ETI. Fitness is a property of a token particle (or particle type) during the early stages of an ETI. After an ETI is complete, it supposedly becomes a property of the Darwinian collective. Particles consequently relinquish their fitnesses. We find this move from epistemological indicator to ontological generator deeply problematic. Many might nevertheless argue that the fitness-transfer framework can still provide us with an adequate indicator for ETIs. This reply suggests a deflationary interpretation of the framework, one stripped of its metaphysical undertones. We now pose two challenges to the adequacy of the fitness-transfer framework, even in its more limited guise as a mere indicator of ETIs.

Let us call the first challenge faced by the fitness-transfer framework “the problem of false positives.” The allegation here is that the set of jointly sufficient conditions it proposes is too permissive. These conditions could mistakenly identify some instances of apparent “fitness transfer” as genuine ETIs. Consider a generic case. Suppose we have a collection of particles that are engaged in particle-particle interactions of positive effect. Conspecific mutualistic interactions represent a form of population structure with obvious effects on particle fitness. Populations whose members exhibit selectively altruistic behavior would be an instance of this. Whenever there are particle-particle interactions with positive effect, isolating a particle from its network will reduce its (counterfactual) fitness. An observer could decide to partition this population into “collectives” based on spatial proximity. Another observer could decide to draw collectives in a different way. However, these collectives would then be drawn on a conventional rather than factual basis. In both cases, one would observe a difference between the counterfactual measure of fitness and the measure in the collective, where the former would have a lower value than the latter.³ Despite the difference, in this example, no ETI has occurred. It is simply an instance of a “viscous” or “neighbor structured” population (Birch 2017; Bourrat 2021; Godfrey-Smith 2008).

A second example of false positives comes from Black et al.’s (2020) discussion of ecological scaffolding. They begin by asking us to consider the imposition of population structure on particles that grow at different rates. Features of the local ecology impose structure on particles by organizing them into collectives that dwell on patches with limited resources. This type of ecology-driven population structure is not uncommon in nature. The transient tidal pools that remain as the ocean tides recede are but one illustrative example. Once collectives are formed, there is no particle migration between collectives. Now, if particles overexploit the resources in

² Constraints of length prevent discussion of this issue. Interested readers should consult Bourrat (2021).

³ This point is related to the debate between pluralists and realists about levels of selection. For a short introduction to this debate, see Okasha (2006, ch. 4).

their patch, the entire collective dies. If, however, a collective survives a particular period, it can then establish new collectives (i.e., reproduce) as a function of the number of particles that are still alive on the patch. That is, the greater the number of surviving particles on a patch, the higher the collective's probability of having particles to successfully "seed" a new patch elsewhere. In this scenario, selection will favor lower particle-level fitness because it increases the probability of collective-level persistence. Collectives that persist longer (up to a point) tend to have a better chance of persisting until the time when collective-level reproduction becomes possible. For example, the optimal duration of time for collectives formed through tidal pooling would be to persist until the tide once again rises. Selection for lower particle-level fitness within a collective consequently favors higher collective-level fecundity using persistence.

This case, like the previous one, appears to meet the two criteria for an ETI that the fitness-transfer framework has established. There is clearly selection for lower particle-level fitness (growth rates) with the imposition of population structure. Particles have apparently made the fitness "sacrifice" that is required to open the possibility of transfer to the collective level. There has also been a proportional increase to collective-level persistence and, even more importantly, reproduction. Collectives seemingly exhibit the type of differential reproductive rates that are needed to distinguish them as evolutionary individuals (Darwinian collectives). Despite meeting these conditions, collective-level aggregations in this case exhibit only "Darwinian-like" rather than genuine Darwinian properties (for details, see Black *et al.* 2020; Bourrat 2022). There are no genuine higher-order (evolutionary) individuals. To see this, we need only imagine what would happen if the structure-imposing ecology is removed. If there were no mechanisms of pooling, there would be no corresponding collective-level structure. The total population of all particles would experience pure competition in which selection favors particles with higher growth rates. Many would argue that evolutionary individuals must, at minimum, maintain their organizational integrity. While transient aggregations are an integral part of an ETI for Black *et al.* (2020), the fitness-transfer framework does not allow us to distinguish this *initial step* in the process from the *completed product* that would be an ETI. Any accidental transient aggregation, even if not in fact undergoing an ETI, must purportedly realize an ETI.

There is yet another, more foundational, challenge to the fitness-transfer framework. The problem is one of discerning the proper reference environment for selection. The proposed framework requires comparing the measures of average particle-level fitness (growth rate) from what appear to be two distinct selective environments (Brandon 1990). As noted in the first step, particle-level fitness is calculated for an *in situ* collective over the long term. The second step of the framework, in contrast, requires calculating particle-level fitness in an experimentally induced "counterfactual" environment that is designed to mirror the conditions of an ancestral selective environment. An unforeseen dilemma surfaces as a direct consequence of the demand that there be two distinct measures of fitness.

On one horn of the dilemma, it looks as if the calculation of particle fitness for an *in situ* collective necessarily assumes a different selective environment for calculations of "counterfactual" fitness. Fitness for entities at any level is commonly conceived of and calculated as a probabilistic expectation over the long run. In much of the

philosophical literature, many have argued that fitness is best understood as the cause of selective evolution. Some contend that it fulfills this role through being a dispositional property of individuals or a propensity (Pence and Ramsey 2013). Others less enamored with the metaphysical commitment to propensities nevertheless share the feeling that a causalist construal of fitness is crucial but prefer to explicate the notion as a compositional property of “organism-environment histories” (Abrams 2009). Setting aside subtle differences of philosophical interpretation it is evident that calculations over the long run must average over many if not all possible selective environments. This is unarguably a key feature for most measures of fitness in the biological literature. The measures used by theoreticians (e.g., Malthusian parameter) average over many selective environments when deriving fitness values including those “counterfactual” states of affairs in which there is no structure or reproduction at the collective level. It would be highly objectionable to rule these out when calculating average particle fitness *in situ*; for it is precisely those conditions that are assumed to be ancestral for derived higher-order entities (i.e., Darwinian collectives). The calculation of “counterfactual” particle fitness consequently averages over only a proper subset of the environments that are used when calculating average particle fitness *in situ*. It thereby neglects relevant events (e.g., collective-level death events). If the foregoing is correct, however, the average particle-level fitness differences that the fitness-transfer framework requires (from steps 1 and 2) will turn out to be illusory because impossible. There can be but a single average selective environment in the long run, and only one corresponding value of fitness for each particle variant in that environment.

To shield the fitness-transfer framework from this worry, advocates might simply “bite the bullet” by maintaining that there are, in fact, two unequal and incommensurable selective environments. Herein lies the other horn of the dilemma. If they adopt this stance, an obvious but unwelcome fact confronts them. Discrepancies in average particle-level fitness across environments containing unique suites of selection pressures *are the expectation*. These differences cannot then, at least without further argument, be presented as uniquely indicative of ETIs. The supposedly incisive dynamic exemplified by differences in particle-level fitness (third step of the framework) seem to be anything but explanatory in this case. Those who study ETIs want to know how average particle-level fitness in an ancestral environment can be (causally) linked to fitness differences in the other. The target of explanation is the *process of transition* to a higher level of evolutionary individuality. We want to know exactly what aspect of collective settings initially serves particle fitness in the long run. Why have the complex forms of life that we observe evolved? Why were particles inclined to form and maintain the sorts of structure that are phylogenetically entrenched by entire clades and their respective taxa? We gain no insight into any of this if we are told merely that there are differences in average particle-level fitness in two incommensurable selective environments. In the end, neither horn of the dilemma proves to be an acceptable one for proponents of the fitness-transfer framework.

4. Conclusion and prospects: A trait-based view of ETIs

In this article, we have established the conceptual structure of the fitness-transfer framework, which is currently the prevailing scheme for identifying ETIs. As already

discussed in section 2, it involves three key steps. The all-important final step requires (1) comparing measures of long-run particle fitness with its “counterfactual” counterparts to determine whether there is a “sacrifice” of particle-level growth rate *in situ*, and (2) that there is proportional compensation for this “sacrifice” in growth rate at the collective level. In the previous section (section 3), we provided several reasons for rethinking the sufficiency of these criteria. There are clearly instances where the fitness-transfer framework would, by its own criteria, be forced to conclude that an ETI has taken place even though there is evidently no genuine ETI. We also presented a dilemma for the fitness-transfer framework that arises from its commitment to the existence of distinct measures of particle-level fitness. In this concluding section, we will briefly introduce a way forward for the study of ETIs.

Considering the problems posed for the fitness-transfer framework, how should those interested in explaining ETIs proceed? For reasons noted in section 3, the primary obstacle for that framework is its heavy reliance on the notion of fitness. We share the conviction that fitness is a crucial notion for evolutionary population biology. However, measures of fitness are not particularly helpful when it comes to identifying ETIs. Observed asymmetrical changes in fitness (i.e., “up” for a collective, “down” for constituent particles) are clearly insufficient for identifying whether ETIs occur. Moreover, as offering only a scalar-valued quantity, a fitness measure conveys very limited information about the diverse mechanisms that might account for ETIs.

The groundwork for a more promising mechanistic approach has already been established (Bourrat *et al.* 2022; Doebeli *et al.* 2017). What distinguishes this type of approach is its emphasis on traits other than fitness. Perhaps the most obvious candidate traits would be those that feature in a decomposition of fitness into vital demographic rates such as those that feature in the fundamental trade-offs of life-history theory (Stearns 1992): survival, growth, birth, and mortality rates.⁴ In this respect, we do not differ from the fitness-transfer view put forward by Michod and collaborators. The basic strategy begins by considering some combination of traits. These traits are mapped onto a (multidimensional) fitness landscape for “ancestral” or “free-living” particles. This same combination of traits is then mapped onto a fitness landscape for “derived” or “collectively embedded” particle fitness. Let us call these landscapes “Landscape1” (blue) and “Landscape2” (orange) in Figure 1, respectively. It is unrealistic to assume that the peaks on these landscapes must coincide, as what is optimal for a unicellular organism need not be optimal for a multicellular one. During the early stages of an ETI, particles will likely be in the near vicinity of optimum growth rate for free-living particles on the peak on Landscape1. As particles become collectively embedded, continuously occurring mutations will likely move some particles away from the optimum of Landscape1 and “relocate” them on Landscape2 (❶ in Figure 1). In doing so, these mutations release the mutant unicellular organisms from some of the constraints associated with unicellularity, at which point the mutants start optimising the traits on Landscape2 (going up the slope ❷ in Figure 1). Landscape1 consequently becomes “counterfactual” in the sense that it no longer has any causal influence on the evolutionary trajectory of average particle fitness.

This trait-based scenario is consistent with the observation that counterfactually free-living (particle-level) fitness decreases while collectively embedded particle fitness increases. It is sufficient for capturing the pivotal dynamics that supposedly

⁴ Such a decomposition could accommodate as many specific traits as needed.

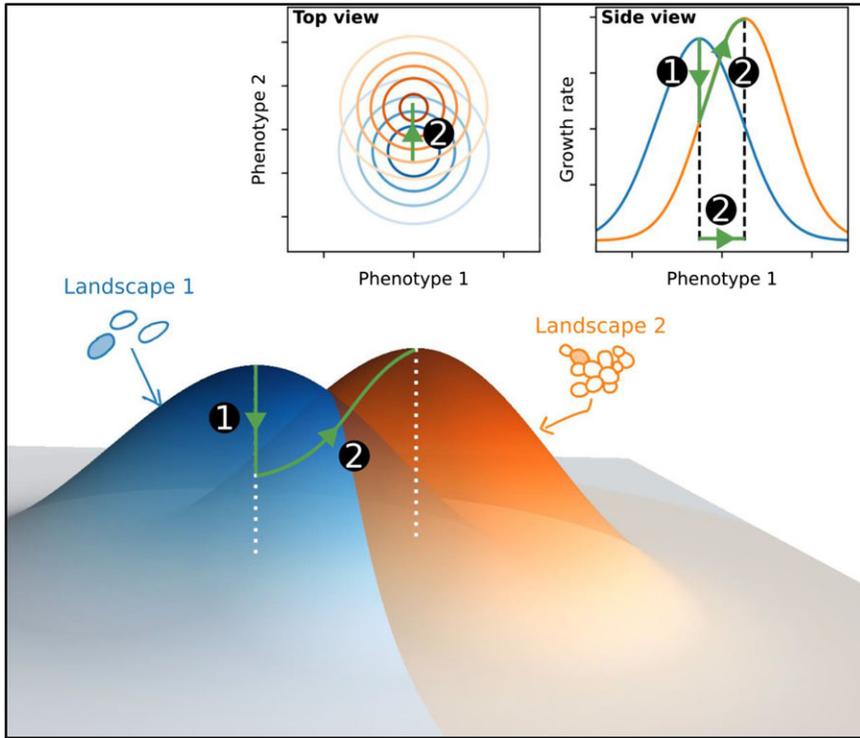


Figure 1. Selective dynamics relating the fitness of ancestral, free-living particles (Landscape 1) to the fitness of derived, collective-bound particles (Landscape 2). See main text (Section 4) for details (color online).

underpin ETIs. However, in this picture, particle fitness and collective fitness are always commensurate. This contrasts with what the export-of-fitness view promulgates. It relies instead on how the two fitness landscapes relate to one another. There is no direct causal relationship between counterfactual fitness and the observed changes in traits. Relative changes in fitness follow from changes in environmental conditions and genetic and phenotypic constraints on the particles.

There is obviously more to be said about this mechanistic, trait-based framework for detecting ETIs. That the suggested approach promises to resolve outstanding difficulties in a way that is consistent with empirical observations is already a mark in its favor. Even more appealing is the fact that it can do so without invoking the literal “export” or “transfer” of fitness.

References

- Abrams, Marshall. 2009. “Fitness ‘Kinematics’: Biological Function, Altruism, and Organism–Environment Development.” *Biology & Philosophy* 24:487–504. <https://doi.org/10.1007/s10539-009-9153-2>
- Birch, Jonathan. 2017. “Kin Selection, Group Selection, and the Varieties of Population Structure.” *The British Journal for the Philosophy of Science* 71:259–286. <https://doi.org/10.1093/bjps/axx028>
- Black, Andrew J., Pierrick Bourrat, and Paul B. Rainey. 2020. “Ecological Scaffolding and the Evolution of Individuality.” *Nature Ecology & Evolution* 4:426–436. <https://doi.org/10.1038/s41559-019-1086-9>

- Bourke, Andrew F.G. 2011. *Principles of Social Evolution*. Oxford: Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199231157.001.0001>
- Bourrat, Pierrick. 2021. *Facts, Conventions, and the Levels of Selection*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/9781108885812>
- Bourrat, Pierrick. 2022. "Evolutionary Transitions in Individuality by Endogenization of Scaffolded Properties." *The British Journal for the Philosophy of Science* 35:719118. <https://doi.org/10.1086/719118>
- Bourrat, Pierrick, Guilhem Doulcier, Caroline J. Rose, Paul B. Rainey, and Katrin Hammerschmidt 2022. "Tradeoff Breaking as a Model of Evolutionary Transitions in Individuality and Limits of the Fitness-Decoupling Metaphor." *ELife* 11:e73715. <https://doi.org/10.7554/eLife.73715>
- Brandon, Robert N. 1990. *Adaptation and Environment*. Princeton, NJ: Princeton University Press.
- Clarke, Ellen. 2013. "The Multiple Realizability of Biological Individuals." *The Journal of Philosophy* 110:413–435. <https://doi.org/10.5840/jphil2013110817>
- Damuth, John, and I. Lorraine Heisler 1988. "Alternative Formulations of Multilevel Selection." *Biology and Philosophy* 3:407–430. <https://doi.org/10.1007/BF00647962>
- Doebeli, Michael, Yaroslav Ispolatov, and Burt Simon. 2017. "Towards a Mechanistic Foundation of Evolutionary Theory." *ELife* 6:e23804. <https://doi.org/10.7554/eLife.23804>
- Doulcier, Guilhem, Katrin Hammerschmidt, and Pierrick Bourrat 2022. "Division of Labor and Fitness Decoupling in Evolutionary Transitions in Individuality." In *The Evolution of Multicellularity* (pp. 227–248), edited by M. Herron, W. C. Ratcliff, and P. L. Conlin. Baton Rouge: CRC Press.
- Folse, Henry J., and Joan Roughgarden. 2010. "What Is an Individual Organism? A Multilevel Selection Perspective." *The Quarterly Review of Biology* 85:447–472. <https://doi.org/10.1086/656905>
- Godfrey-Smith, Peter. 2008. "Varieties of Population Structure and the Levels of Selection." *The British Journal for the Philosophy of Science* 59:25–50. <https://doi.org/10.1093/bjps/axm044>
- Hammerschmidt, Katrin, Caroline J. Rose, Benjamin Kerr, and Paul B. Rainey 2014. "Life Cycles, Fitness Decoupling and the Evolution of Multicellularity." *Nature* 515:75–79. <https://doi.org/10.1038/nature13884>
- Maynard Smith, John, and Eörs Szathmáry. 1995. *The Major Transitions in Evolution*. Oxford: W. H. Freeman. <https://doi.org/10.2307/2935266>
- Michod, Richard E. 2005. "On the Transfer of Fitness from the Cell to the Multicellular Organism." *Biology and Philosophy* 20:967–987. <https://doi.org/10.1007/s10539-005-9018-2>
- Michod, Richard E., Aurora M. Nedelcu, and Denis Roze 2003. "Cooperation and Conflict in the Evolution of Individuality: IV. Conflict Mediation and Evolvability in *Volvox Carteri*." *Biosystems* 69:95–114. [https://doi.org/10.1016/S0303-2647\(02\)00133-8](https://doi.org/10.1016/S0303-2647(02)00133-8)
- Okasha, Samir. 2006. *Evolution and the Levels of Selection*. Oxford and New York: Clarendon Press and Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199267972.001.0001>
- Pence, Charles H., and Grant Ramsey. 2013. "A New Foundation for the Propensity Interpretation of Fitness." *The British Journal for the Philosophy of Science* 64:851–881. <https://doi.org/10.1093/bjps/axs037>
- Shelton, Deborah, and Richard E. Michod 2014. "Group Selection and Group Adaptation during a Major Evolutionary Transition: Insights from the Evolution of Multicellularity in the *Volvocine* Algae." *Biological Theory* 9:452–469. <https://doi.org/10.1007/s13752-014-0159-x>
- Shelton, Deborah, and Richard E. Michod 2020. "Group and Individual Selection during Evolutionary Transitions in Individuality: Meanings and Partitions." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375:20190364. <https://doi.org/10.1098/rstb.2019.0364>
- Stearns, Stephen C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Takacs, Peter, and Pierrick Bourrat 2022. "The Arithmetic Mean of What? A Cautionary Tale about the Use of the Geometric Mean as a Measure of Fitness." *Biology & Philosophy* 37:12. <https://doi.org/10.1007/s10539-022-09843-4>

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