**Review of Javier Suárez and Elisabeth A. Lloyd, *Units of Selection*. Cambridge: Cambridge University Press, 2023, 75 pp, £49.99 HB**

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This book defends the ‘disambiguating project’ (DP) with respect to the units of selection, the thesis that the expression ‘units of selection’ is polysemous, in that it ‘refers to at least three non-co-extensional functional concepts: interactor, replicator/reproducer/reconstitutor, and manifestor of adaptation/type-1 agent’ (1). Lewontin (1970) inaugurated the ‘recipe’ approach to the units of selection issue, the idea that we can identify a small number of conditions, such as variation, differential fitness, and heritability, individually necessary and jointly sufficient for natural selection to take place, and for units of selection to be identified. Later, Hull and Dawkins argued that ‘units of selection’ could refer to either ‘replicators’—entities that pass on their structure in replication—or ‘interactors/vehicles’—entities whose interaction with the environment causes replication to be differential. Subsequently a third entity was added: ‘manifestors of adaptation/type-1 agents’, entities that are cohesive and exhibit accumulated engineering adaptations.

In recent years there have been influential critiques of the Hull-Dawkins framework (e.g. Okasha 2006, Godfrey-Smith 2009), and defences of versions of the simpler recipe approach, though not necessarily Lewontin’s version. Suarez and Lloyd call this the UP, ‘unitary project’. They argue that the rejections of the bipartite/tripartite approach are mistaken. We need the DP, they claim, to do justice to the varying legitimate projects and research questions that biologists can and do pursue regarding the units of selection.

This book is complex, dense, and highly specialised. One suspects it would be largely incomprehensible and of limited interest to those not already well-versed in the units of selection literature. But for the cognoscenti, it is a very interesting, sophisticated and well-informed intervention in the current debate, and the authors present a strong case in defence of the DP. Ultimately, however, I was not convinced.

Firstly, it does not necessarily follow from the fact that we need to distinguish replicators, interactors and manifestors that all of these are *units of selection* in different senses, and thus that ‘units of selection’ is polysemous. One could accept the distinction between the types of entities but only regard one of them as the unit of selection. This was the view taken by Gould (2002) and others, who held that only interactors are units of selection, as it is these whose causal interactions with the environment drive the evolutionary process. They are thus the *agents* of selection; replication of replicators is differential *as a result of* selection on interactors, with the latter being the fundamental causal process. Changes at the genic level merely allow us to ‘keep the books’ on evolutionary change: there is selection *for* interactor-properties, but merely selection *of* replicators (Sober 1984). Of course, replicators such as genes may also be interactors, as in cases such as meiotic drive and segregation distortion. But these are exceptional cases, and in such cases the replicators, genes, have the status of units of selection because they are also interactors.

In terms of manifestors of adaptation/type-1 agents, these are a subset of interactors; they are interactors that have evolved engineering adaptations, are particularly cohesive, or have a kind of unity of purpose. They may be the object of study separate from other entities. But one could claim the *reason* they are *units of selection* is that they are interactors, thereby retaining the idea that all and only units of selection are interactors. If the manifestor of adaptation idea is a way to avoid the mistake that some seem to make in suggesting that all interactors and units of selection need to be cohesive in a strong sense, and to have evolved engineering adaptations, that is a laudable role for it, but it does not have to follow that the manifestor of adaptation is a separate or special type of unit of selection in its own right. Thus, Suarez and Lloyd talk of ‘the existence of these two types of units’ (35), interactors and manifestors, but if manifestors are a subset of interactors, it is misleading to talk of *two types* of units here. Dogs and mammals are not really ‘two types of animals’.

Alternatively, one could take the view that Dawkins seemed to have taken at one point, that while we need to distinguish replicators and interactors, what he called ‘vehicles’, replicators are the only true units of selection. While there is vehicle selection of a sort, vehicles are only units of selection by courtesy or in a derivative sense: the fundamental selection process takes place at the replicator level. I am not endorsing any of these views, merely pointing out that they are all seemingly consistent with the bipartite or tripartite framework, such that the latter does not entail the DP: more is needed to show that all of these entities are or can be *units of selection*, and that ‘units of selection’ is polysemous.

In response to worries about including the replicator concept in an abstract characterisation of natural selection—in particular the fact that the existence of replicators understood as entities possessing properties such as high-fidelity copying mechanisms would seem to be a *product* of selection rather than a *precondition* of all selection processes—Suarez and Lloyd recommend broadening the notion out to include ‘reproducers’, in the sense of any entities that are able to reproduce in the fairly familiar sense. Multicellular organisms may not be replicators, but they are reproducers, forming parent-offspring lineages. But this involves a dramatic weakening of the replicator concept, such that it is unclear now whether they are saying anything more than the humdrum claim, always recognised by the recipe approach, that for a selection process to take place there need to be entities that reproduce. For there to be heritable variation in fitness at a level, there seemingly need to be reproducing entities at that level. But this does not imply that the reproducers are units of selection in a distinct sense from the interactors. It could be that the interactors *must also be reproducers* in order for selection to take place. This is essentially Godfrey-Smith’s view, though he does not like the interactor concept, suggesting we replace it with the concept of a Darwinian individual.

It might be argued that a counterexample to the claim that all interactors are reproducers can be found in multi-level selection type 1 (MLS1) processes, where the collectives are interactors but only the particles composing them are reproducers. But this is not the only way of thinking of MLS1 processes. I have argued elsewhere (Boucher 2023) that in MLS1, the particles are the interactors, not the collectives, and thus MLS1 counts as particle, not collective selection. Indeed, in ‘Units and Levels of Selection’, Lloyd (2017) seems to agree: ‘under MLS1, the lower-level particles are the interactors as well as the replicators, while in MLS2, both the upper-level collectives as well as the particles are interactors.’ To be sure, entities may reproduce without being independent interactors. From the fact that all interactors are reproducers it does not follow that all reproducers are interactors. But it is not clear why such reproducers should be thought of as units of selection.

So it seems to me that views such as Godfrey-Smith’s may survive Suarez and Lloyd’s critique. According to Godfrey-Smith, something is a paradigm unit of selection, i.e., a Darwinian individual, when, put in Suarez and Lloyd’s terms, it is simultaneously a reproducer, an interactor, and a manifestor of adaptations, at least with respect to reproduction. Suarez and Lloyd argue that Godfrey-Smith must implicitly accept that there are different research questions relating to reproducers and interactors as he distinguishes selection from heritability (61). But from the fact that he accepts that there has to be heritability, and hence reproduction—and hence reproducers—for natural selection on Darwinian individuals, it does not follow that the DP is correct. From the fact that Darwinian individuals, one type of unit, must reproduce, and give rise to parent-offspring similarities, it does not follow that interactors and reproducers are distinct kinds of units of selection.

In adjudicating between the two projects (UP and DP), certain theoretical virtues may play a role. The UP, especially in Godfrey-Smith’s work, has the virtues of simplicity, elegance, and unifying power. Much about natural selection and the evolutionary process is, seemingly, captured and explained using minimal resources, and a minimal number of entities, in Godfrey-Smith’s Darwinian-population framework. It is ontologically parsimonious. The DP, by contrast, is complex and inelegant. It multiples entities, possibly beyond necessity, and it posits multiple ambiguity where others see none. Its adherents will, of course, claim that to the extent that it has these drawbacks, they are outweighed by other virtues the DP possesses, in particular, in allowing us to recognise a number of different units of selection research questions that are obscured by the UP and its, as they see it, excessive focus on the Evolutionary Transitions in Individuality (ETI) project as the be all and end all of evolutionary research. I cannot adjudicate this issue here. I merely wish to draw attention to some of the meta-level and methodological considerations that must be in play in any such assessment.

There are a few errors in the book. On page 19, they follow Griesemer in claiming that the bipartite framework is superior to the recipe approach because it is more abstract, and does not build in facts about things about genes and organisms. But this is also true of the recipe approach: Lewontin’s three conditions, variation, heritability, and differential fitness, are entirely abstract, and do not mention anything about ‘specific biological objects already known to the biologists’ (19).

At times the structure of the book was a bit puzzling. Section 3 has a heading relating seemingly only to material coming before 3.1, with 3.1 then being on a different topic; the heading of 3 needs to relate to all of Section 3.

On page 28, they say that identifying a manifestor of adaptation is sufficient for there to have been interactors involved in the selection process because an interactor ‘may’ have been involved in the process that produced the engineering adaptation. But for the sufficiency to hold this ‘may’ would need to be a ‘must’.

On page 40, they claim replicators are abstract objects, but presumably what they mean is the replicator concept specifies an abstract functional role that can be filled by various concrete objects, not that any replicators are abstract objects in the way numbers are.

On page 48, Buss’ (1987) book is bizarrely referred to as ‘his Element’.

In closing, this book will be of great interest to those working on the units of selection problem and related issues such as the major transitions in evolution and the metaphysics of biological individuality. It presents a carefully-argued case in defence of the DP, which adherents of the UP will need to take seriously in subsequent work.

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