Introduction

This Element introduces what we call the disambiguating project (DP) about the units or levels of selection. By the DP we mean the thesis that the expression 'units of selection' refers to at least three different non-co-extensional functional concepts: interactor, replicator/reproducer/reconstitutor, and manifestor of adaptation/type-1 agent. We present each of these concepts and demonstrate the necessity of their isolation because each of them responds to a distinct question about the units of selection, and these distinct questions are not always posed in combination in today's biological research. We further apply our framework to the study of the debates concerning the evolutionary transitions in individuality (ETI) and argue that the DP interprets the ETI better than any project rejecting the polysemy (multiple meanings) of the expression. Thus, we claim that the differentiation between at least three functional concepts equivocally meant by the expression 'units of selection' is fundamental to clarify some conceptual confusions in biology, which we argue rest on the conflation of these distinct meanings.

Our project is partially presented as a response to some criticisms by some recent approaches to the study of units that treat the expression as unambiguous. We refer to the latter as the unitary project (UP), a project that has its origin in Lewontin's formulation of the problem of the units of selection in 1970, but that has substantially evolved afterwards. While authors working under the UP find that the expression 'units of selection' may be confusing and requires philosophical treatment, they reject that it stands for more than one concept. Under the UP, disagreements about the units may rest on confusions over the application of *the* concept to different cases, or on empirical disagreements, but are not the result of a conceptual conflation of different meanings under the single expression 'units of selection'. We demonstrate that adopting a UP is not a profitable research avenue to treat the debates about the units of selection, and acknowledging that the expression stands for different functional concepts is essential for proper communication among today's scholars.

Our agenda is as follows: we first introduce our proposal and review some of the historical origins of the DP, and its conceptual relationship to Lewontin's original version of UP, the so-called recipe approach. We argue that the DP does not *oppose* the recipe approach, but rather specifies and connects it to several lines of biological research. We demonstrate the value of using the DP, rather than the UP, by demonstrating that recent evidence from biology and philosophy shows the continuing necessity of distinguishing different non-co-extensional meanings of the expression 'units of selection' to clarify today's debates in biology. More specifically, we show that in today's biological

research – especially when properly framed under the adaptationist versus the evolutionary change school of evolution – the expression 'units of selection' refers to at least three different types of distinct functional concepts: interactors, reproducers/replicators, or manifestors of adaptation/type-1 agents. We isolate and analyze these concepts, and argue that each of them singles out a set of independent research questions that can be asked, *either singly or in combination*, about the action of natural selection.

We argue further that the failure to appreciate the existence of the multiplicity of meanings and concepts that we advocate in this work derives from a series of *misconceptions about the DP*. All of these misconceptions are ultimately grounded on an excessive and misguided emphasis on reducing all questions about units to questions framed only under the single adaptationist and reproduction-centred project of the ETI. We contend that this emphasis has caused the emergence of an eliminative version of the UP, which we argue is not a profitable research avenue, neglecting a substantial amount of contemporary biological research about units not directly concerned with the origin of the reproductive hierarchy. We show that the changes involved in the ETI can be straightforwardly analyzed under our version of the DP, and in a more illuminating manner than they are thought of when they are conceived under the tenets of a UP. We thus conclude that the DP is the most adequate way of addressing today's philosophical debates about units.

Highlights

- We distinguish two types of projects about the units of selection: the DP and the UP.
- The DP seeks to clarify different non-co-extensional meanings of the expression 'units of selection' that are used in different research projects.
- The UP conceives that the debate about units only encompasses one type of unit, and its purpose is finding criteria to determine whether an object is a unit of selection.
- We review the DP in a historic-systematic way and demonstrate a tripartite version of it as the most profitable way of characterizing the units of selection debates.
- We relate the DP to Lewontin's recipe approach to the levels of selection and show that the former is a specification of the latter.
- We argue that the criticisms of the DP are ungrounded and based on misunderstanding of the framework.
- We argue that the tripartite version of the DP that we defend can be used to gain a better understanding of the debates about the ETI.

1 What Is a Unit of Selection and How Can We Identify It? The Disambiguating and the Unitary Projects

The units or levels-of-selection debate concerns the type of biological forms of organization that can evolve by means of the process of natural selection, originally described by Charles Darwin in *The Origin of Species*. According to Darwin's process, under ideal conditions, the traits of a biological form of organization (e.g., organisms and colonies) that are systematically linked to the fitness of their bearers and confer on them a relative fitness advantage with relation to other members of their population will spread in the population until they become the predominant forms (Box 1).

Darwin's process is additionally the basic schema for explaining the existence of highly sophisticated traits that make some organisms – or alleles, groups, or colonies – look as if they were engineered to fit their environment (engineering/trans-temporally accumulated adaptations). For example, it is used to explain why anteaters have their characteristic elongated noses and tongues way longer than their heads and lips, but no teeth in their mouths. Or why vampire bats have their teeth, sensory apparatus, kidney, and bladder adapted for a purely blood-sucking diet. Or how collared flycatchers have their characteristic coloured patterns, especially their spectacular white collar. The explanation of why all these organisms and their populations possess these phenotypic characteristics lies in a basic idea: these spectacular traits are connected to the relative fitness of these organisms and their populations, such that anteaters with the aforementioned characteristics reproduced more than those that lacked them, until a point where the traits become the only extant forms in the population of anteaters. The same would be true for the traits of vampire bats and flycatchers.

An intriguing philosophical question about the units of selection concerns *the ways of singling out* the biological forms of organization that have the required properties to be causally affected by natural selection and/or to evolve by natural selection. This fundamental philosophical question cannot be divorced from the *biological question about what natural selection is*, for the way in which one replies to the latter is intimately connected to how one replies to the former, as we will show. So, the question about the units of selection is in the end simultaneously a question about how the process that Darwin described in *The Origin of Species* should be understood. In other words, we have to know *what the process really is*, before we can understand the *best ways to look for it*.

A long tradition in philosophy of biology that dates back to the early works of Dawkins (1976) and Hull (1980), and continues with the works of Wimsatt (1980a, 1980b); Brandon (1981); or Lloyd (1986, 1988/1994, 1992, 2001, 2023; Lloyd and Wade 2019) conceives that the philosophical question about the units

Box 1 Darwin's process and the evolutionary process are not the same

It is sometimes mistakenly assumed that Darwin's process (or evolution by natural selection) is equivalent to the evolutionary process, or, to put it differently, that evolution is made up only of evolution by natural selection. This is however a misconception of the aims of contemporary evolutionary research. Contemporary evolutionary research is concerned with the study of several processes and mechanisms (or, more generally, *evolutionary factors*) that change the composition of biological populations over time differently, sometimes in combination favouring the same type of changes, but others with some processes opposing the direction of others.

Some of the evolutionary mechanisms, like genetic mutations, recombination, or genetic drift, affect the pattern of inheritance, and in doing so affect the evolutionary process. Others, like niche construction, phenotypic plasticity, or other developmental processes, affect the patterns of expression of traits, and in doing so they also affect the evolutionary process. Finally, a third group of processes includes phenomena like phyletic inertia, evolutionary trade-offs, or some developmental constraints (see Keller & Lloyd 1992, for discussion of these concepts), which affect the composition of biological populations by opposing certain types of changes due to the intrinsic configuration of the entities composing the biological population.

Under this perspective, the aim of evolutionary biology is to explain the history, relatedness, and the forms and function of life on Earth (e.g., Hull 1988a; Gould 2002; Lloyd 2015, 2021), but without necessarily highlighting the influence of one mechanism – natural selection – or one specific output – engineering/trans-temporally accumulated adaptations – over the rest. In this complex view of the evolutionary process, Darwin's process of natural selection is a way of affecting the evolution of a population by favouring the trait variants that increase the fitness of their bearers. But Darwin's process alone does not *solely determine* the composition of biological populations, or how they change over time, because the type of variants it favours may interact with or be opposed by any other evolutionary process. This Element is only dedicated to the study of the Darwinian process, so our analysis may rest on some idealizations which we do not want the reader to misunderstand.

of selection invites a project for distinguishing or disambiguating different meanings of the expression. Under this project, it is assumed that biologists and philosophers sometimes disagree about what the units of selection are because they mean different concepts by the same expression. Thus, part of

the disputes about the units may fade away as soon as one realizes that some researchers are pursuing different legitimate questions, each of which triggers a different debate.

The task of a philosopher working under this type of project would consist in disambiguating the different meanings of the expression – that is, they would clarify the polysemic character that 'unit of selection' can adopt in different research contexts. A central guiding assumption of some researchers working under this tradition is the acknowledgement of the existence of at least two different approaches to evolution – later characterized as the distinct Adaptationist and Evolutionary Change Schools – each guided by a different set of research problems (e.g., Wimsatt 1980a, Griesemer 2000a, 2005; Wade, 1978, 2016; Lloyd 1988/1994, 2023). We refer to the project carried under this prior long tradition as the DP (Box 2).

In contrast, researchers from the adaptationist tradition of the study of ETI or Major Transitions in Individuality have recently denied the polysemy of the expression; they argue that the meaning of 'unit of selection' is unambiguous. They believe there are *not* several philosophical questions about the units, *but a single one* (Okasha 2006; Godfrey-Smith 2009, 2013, 2015).[1] Researchers working under this second project accept that there can be ambiguities or disagreements about *how best to characterize the unit of selection*. But they disagree with those working under the DP that these disagreements rest on a conflation of different concepts or questions under the expression 'units of selection'. In their view, the question is simply *singular*, and the debate is about *one* type of unit whose properties must be discovered. We refer to this tradition as the *unitary project*. Such a view has recently been expressed by Godfrey-Smith, who claims:

> Questions about the "unit" of selection *are not ambiguous*; the units in a selection process are just the entities that make up a Darwinian population at that level. (Godfrey-Smith 2009, p. 111, emphasis added)

The task of a philosopher working under the UP tradition would be to uncover the set of properties that are necessary and sufficient to argue that the entities at one specific level are units of selection (Box 3). We will later show that a peculiarity of researchers working under this tradition is that they neglect the existence of different schools of evolution, each guided by a different research programme aimed at replying to different research questions.

Researchers working under the UP have posed several criticisms to the usefulness and necessity of the DP for today's biological research, some of

[1] But see Griesemer's analysis of ETIs (2000a, 2000b, 2005) for exceptions to this tendency to reduce the questions about units to a single problem.

Box 2 A brief introduction to the types of units that we distinguish in this work

We distinguish three functional meanings of the expression 'units of selection', each of which would capture a special set of research questions that can be asked either singly or in combination. These meanings are:

(a) Interactor: Units that interact with the environment in such a way that replication or reproduction is differential. The interactor captures the trait–environment relationship and its effects over the differential fitness of bearers of the trait.

For example, the members of the moth species *Biston betularia* would act as interactors in the classic selection processes such as industrial melanism, in which changes in environmental pollution triggered a fitness advantage for darker moths. Note that while *B. betularia* is an interactor with respect to its colour, it simultaneously has a 'product-of-selection adaptation', since no *new* mechanisms or properties are evolved in, that is, introduced into, the selection process producing the increased frequency of dark moths in the population. The only thing that has changed as a result of the selection process is the *frequency* in the population of dark moths; their biology is unchanged.

(b) Manifestor of adaptation/type-1 agent: A manifestor is a unit where a selection process has acted/acts consistently over time resulting in the accretion of a new mechanism or new process not seen before in the lineage, that is, in a tinkering/engineering or trans-temporally accumulated adaptation. A type-1 agent is a subclass of the manifestor in which the optimization of several traits at the level seems obvious, and where the history and accumulation of selection is responsible for such optimization.

For instance, bee colonies are manifestors of adaptation with respect to the bearded sting of individual bees. In this case, the colony is the manifestor of adaptation because the sting shows optimization at the colony level insofar as its use causes the death of individual bees while simultaneously protecting the colony. On the other hand, humans function as manifestors of adaptation *and* type-1 agents with respect to their eyes, as the eye shows a clear history of optimization and trans-temporal accumulation of multiple traits across phylogenetic history.

(c) Replicator/reproducer/reconstitutor: Unit that gets differentially copied (replicator), differentially transmitted through material overlap (reproducer), or differentially recreated in the absence of copy or material overlap (reconstitutor) across generations. This type of unit is responsible for the process of heritability. A unit playing this functional role must be

introduced in the analysis of units to clearly distinguish cases of ontogenesis where changes are due to phenotypic plasticity, from cases where the changes can be due to the action of natural selection (see Keller & Lloyd 1992 for discussion of these concepts).

For example, genes are replicators for traits such as eye colour; gametes or whole cells are reproducers for epigenetic traits such as certain disease susceptibilities in humans; many holobionts (animal or plant hosts plus their microbiome), such as vampire bats, are reconstitutors for traits like sanguivory.

Note that this is only a brief introduction, as the aim of this Element is to make these meanings more precise, while tracing back their historical development and the reasons why they must be kept in mind when analyzing units.

which have not yet received a systematic response. This Element presents a tripartite and functionalist version of the DP against the body of these criticisms.[2] Our tripartite version rearticulates and makes clearer some of the meanings of the expression 'units of selection' originally isolated by a variety of researchers working in the DP tradition. Concretely, we isolate three meanings of the expression 'units of selection' and connect each of them to (i) a specific research question, (ii) the type of evidence required to reply to the research question affirmatively, (iii) the type of modelling practices used to reply to the question, and (iv) the predominant research context where the question is usually asked. Grounded on this, we also show that some of these questions, while conceptually distinct, are asked in combination in research on the ETI.

This Element argues for the necessity of the tripartite version of the DP to solve some of the more pressing debates in today's biology. We focus on debates where biologists disagree because they are using different meanings of the expression 'units of selection'.

Our central message is that the historical proliferation of different versions of the DP since its introduction in the 1980s responds to the existence of different types of research questions in biological research about units, each motivated by different ways of perceiving how the processes of natural selection and evolutionary change ultimately act (Box 1). This variety of factors and processes includes the type of units these processes act upon, the type of outcomes they may produce, and the type of evidence that needs to be gathered to demonstrate

[2] By *functionalist* we mean that each of the meanings we isolate is distinguished by the specific causal role it plays in the process of natural selection.

Box 3 Unit of selection versus level of selection versus target of selection

The expressions 'units of selection' and 'levels of selection' are often used interchangeably (Okasha 2006; Godfrey-Smith 2009; Bourrat 2021; Lloyd 2023), but occasionally they have been used to refer to different concepts (Brandon 1988). As a matter of fact, in biological debates the two expressions are not usually distinguished, being used synonymously by most authors, and sometimes ambiguously with respect to the specific functional meaning intended. As this Element is addressed to these biologists, as well as philosophers of biology interested in these debates, all of which tend not to distinguish the expressions, we will use them interchangeably here.

Metaphysically speaking, however, there are principled reasons to differentiate between them. 'Unit of selection' generally refers to a functional meaning, be it interactor, manifestor/type-1 agent, or replicator/reproducer/reconstitutor, which can apply across different levels of the biological hierarchy. 'Level of selection' and 'target of selection', on the other hand, may be used to refer to a formal role, or a specific level of entity in the biological hierarchy, for example, gene, genome, cell, organism, group, and colony. In this sense, 'unit of selection' would be more general/abstract, and would be the genuine object of philosophical inquiry: how many [functional, formal, or structural] meanings of 'unit' are there? What are the abstract, structural/formal, or phenomenal criteria to distinguish types of units from one another? Are these principled criteria or do some meanings reduce to other meanings? All these constitute genuine philosophical questions about the units.

'Levels of selection' and 'targets of selection', in contrast, could be reserved for the empirical study of the biological objects that may function as units of selection, in any of its meanings: are bee colonies interactors/targets of selection? Are bee colonies also manifestors/type-one agents? Are holobionts reproducers as a whole? Or only partly? All these constitute empirical questions about specific objects in the biological hierarchy.

that selection and/or evolutionary change is acting at that level. In today's biology, we postulate that there are *at least* three, perhaps four or more, non-co-extensional meanings of the expression 'units of selection', each capturing a distinct functional, causal, role that different entities might play in the process of natural selection.

Because we think that the rationale of a research project is not separable from its history, and the type of problems it was aimed to solve when the

project originally started, our argument will be presented historically, roughly in chronological order. However, our main claims will be complemented with evidence directly taken from today's biological research along the way.

In Section 2, we introduce the historical origin of the debate(s) about units of selection and justify the reasons why the DP started. We illustrate how the DP evolved, and how at least three different meanings were isolated.

In Section 3, we systematically introduce the two main sources of misunderstanding in debates about units that we have identified. Based on this, we show evidence of how the meanings we isolated in Section 2, and their related research questions – originally isolated by Lloyd – have been reintroduced under different names by biologists and philosophers in recent years. This reintroduction responds to the perception, by both philosophers and biologists analyzing recent debates about units of selection that it is necessary, to distinguish between different types of research questions at stake in these debates. We take this as evidence that the DP is still necessary, both to avoid misunderstandings and to prevent biologists talking past each other.

In Section 4, we show how the Adaptationist version of the ETI project, which started in the 1990s, wrongly convinced some people that the DP was not necessary anymore, leading to the emergence of a series of UPs. We show, in detail, that those who became convinced that the DP was no longer necessary misconceived some fundamental aspects of the project. More importantly, they wrongly conceived *a (specific) project about the evolution of reproduction* – which is what the adaptationist version of ETI is – as if it encompassed *all the projects about units*. We first offer a reinterpretation of this ETI project under the lens of the DP. We then show that the DP is better suited to capture the complexity of the ETI better than any of the currently extant UPs attempting to frame the ETI project. Finally, we show how even some of those who initially rejected the DP have recently re-introduced some of the concepts originally isolated under the same or different names.

Finally, in Section 5, we conclude that the DP is here to stay. Today's evidence still suggests that the expression 'unit of selection' has at least three meanings, referring to three distinct functional roles that trigger three different types of research questions: interactor, replicator/reproducer/reconstitutor, and manifestor/type-1 agent questions. These different concepts are investigated by different biologists across different schools of evolution. We leave as an open question whether further meanings could be discovered.

2 How the Expression 'Units of Selection' Acquired Its Polysemic Meaning or Why the Disambiguating Project Started

This section introduces the DP in a historic-systematic way. Firstly, we introduce Lewontin's recipe approach as the source of contemporary units of selection debates. We explain the historical and biological reasons why Dawkins and Hull soon perceived the necessity of distinguishing two questions in debates about the units, instead of one as Lewontin's recipe approach implied. We show that Dawkins' and Hull's accounts are not in opposition to the recipe approach, but are a way of specifying its nature. Secondly, we introduce the tripartite Framework in the DP as a way of specifying a further non-co-extensional meaning of the expression 'units of selection' to account for part of the disagreements between researchers working on the evolutionary change school and those working in the adaptationist school of evolution (Section 3). We later show the relationship between the tripartite Framework and the recipe approach, demonstrating that they are compatible and, in fact, complementary approaches to think about units.

2.1 From the Recipe Approach to the Interactor/Replicator Framework

Lewontin (1970) constitutes the classical source for introducing the question about the units of selection as an urgent issue to be resolved in the biological and philosophical agendas. He introduced the debate as follows:

> The principle of natural selection as the motive force for evolution was framed by Darwin in terms of a "struggle for existence" on the part of organisms living in a finite and risky environment. The logical skeleton of his argument, however, turns out to be a powerful predictive system for changes at all levels of biological organization. As seen by present day evolutionists, Darwin's scheme embodies three principles . . .:
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> 1. Different individuals in a population have different morphologies, physiologies, and behaviours (phenotypic variation).
> 2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
> 3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable).
>
> These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change. (Lewontin 1970, p. 1)

Lewontin's conception of the units has been referred to as the 'recipe approach' (Okasha 2006). According to it, identifying a level or unit that is