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INDIVIDUALITY AND SELECTION REDUX

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ABSTRACT

This review offers a critical examination of the relationship between individuality and natural selection. First, I challenge the widely held *Individuality Assumption*—the idea that an entity must be an individual to function as a unit of selection. Through a systematic analysis of the main concepts of units of selection and evolutionary individuals, I show that the Individuality Assumption is untenable: biological entities can play important evolutionary roles in the process of natural selection without qualifying as individuals in any significant sense. Second, I shed light on the conceptual and theoretical relationship between the debates on the units of selection and evolutionary individuality, which have largely grown independently and are often treated separately. Third, I contend that the relationship between individuality and selection is obscured by the tendency to construe evolutionary individuality in terms of evolvability. To overcome this problem, I propose an integrative framework that connects the different concepts of units of selection and evolutionary individuals with a philosophical account of individuality. This framework is visualized in the form of an *Individuality Space* that serves as a heuristic tool to further investigate the relationship between individuality and selection. I illustrate its utility by applying it to evolutionary transitions in individuality.

INTRODUCTION

It seems just natural to think of evolution by natural selection as deeply connected to individuality. Natural selection is essentially the process of sorting certain biological entities: some of them die, some of them live long enough to produce more entities like themselves, and this differential survival and reproduction is what changes the composition of their populations over time and drives evolutionary change. For this to work, then, it is reasonable to think that the entities need to be more-or-less unitary and discrete for them to be sorted out, and they need to be different from one another for the sorting to make an evolutionary difference. In other words, they need to have *individuality*. The main exponent of this way of thinking about individuality and natural selection was David L. Hull (especially in "Individuality and selection," 1980), who argued that "individuality is inherent in selection processes, not incidental to them. If so, then understanding selection processes requires us to understand individuality" (Hull 1992:184). I will call this way of reasoning about the relationship between individuality and selection the 'Individuality Assumption.'

THE INTRICATE RELATIONSHIP OF INDIVIDUALITY AND SELECTION

Yet, once we start asking what kinds of entities can participate in natural selection, how they should be characterized, what roles they play, and how they originate, the apparent simplicity of the connection between selection and individuality begins to unravel. First, there is the problem of what sorts of entities count as individuals and thus participate in natural selection. Typically, organisms have been considered the main candidates, and this aligns with them being regarded as "paradigmatic" individuals (for discussion, see Prieto 2023:34–36). However, evolutionary theory has long recognized additional candidates—genes, groups, symbiotic collectives, and lineages, and among others—whose individuality is more contentious than in the case of organisms. But are things like groups and species *individuals* in

the same sense organisms are—or at least in a sense relevant for evolution by natural selection? Hull argued, as many scholars after him, that the answer is yes: "genes, organisms *and* species, as they function in the evolutionary process, are necessarily spatiotemporally localized individuals. They could not perform the functions which they perform if they were not" (Hull 1978:337; emphasis in the original. Hereafter, emphasis in quotations is as in the original, except where otherwise indicated).

To complicate things further, several of these candidate individuals are compositionally related—thus, genes are housed inside cells, which in turn compose organisms, which take part in groups, which form lineages, and so on. Therefore, there is the possibility that selection acts on more than one of these entities *simultaneously*. Under which conditions this happens, what its evolutionary consequences are, and how the potential conflicts between entities at different "levels" are managed, are all questions discussed under the banners of *group selection* and *multilevel selection* (see Leigh Jr. 2010, Okasha 2006). Notice that here, as in the rest of this article, I use the term 'levels' in the sense of 'particles' and 'collectives' and not in the sense of 'levels of organization' (see Eronen and Ramsey 2025).

But there are yet more difficulties. The literature on the *units of selection* (Suárez and Lloyd 2023) shows that not only can natural selection act on diverse sorts of individuals—some of which don't seem to have much individuality, at least compared to organisms—and in several of them simultaneously, but these might also have *different functional roles* in the process of selection. Some of these individuals might interact with the environment and thus be the kind of things that are targeted by selection, whereas others might be involved in the transmission of variation through replication, and yet others might accumulate adaptations after successive rounds of selection. One and the same individual might fulfil all these roles, but this should not be assumed to be always the case.

Finally, individuality is itself an evolved trait and, arguably, natural selection is largely responsible for its emergence, maintenance, and change. So we might be dealing with a chicken-and-egg situation here: individuality seems to be a prerequisite for entities to participate in natural selection, but natural selection is a prominent factor in the evolution of individuality in the first place (Trestman 2013). These and other problems concerning the evolution of individuality are treated within the literature on the *evolutionary transitions in individuality* (ETI; Griesemer 2000a, Hanschen et al. 2018, Herron 2021, Michod 1999, Michod and Roze 1997, West et al. 2015). According to ETI research, new individuals arise when simpler units integrate to form higher-level entities (e.g., in the evolution of multicellular individuality from unicellular precursors). This idea is tightly linked to the problem of multilevel selection: an ETI involves the shift of selection to the new, upper levels, while selection at lower levels gets suppressed (Bourrat 2015a, Michod and Nedelcu 2003, Okasha 2005, 2022). At least in some lineages, the series of transitions tends to bring individuality closer to that which is characteristic of paradigmatic organisms (Buss 1987, Pepper and Herron 2008).

TOPICS AND AIMS

As we have seen, the relationship between individuality and natural selection is conceptually intricate. I contend that much of the implicit pull behind it stems from the Individuality Assumption, that is, the Hullean claim that for an entity to be subjected to natural selection, it *must be* an individual. But is this widely-held assumption warranted? Credit is due to Stéphane Chauvier for being one of the relatively few scholars to have noticed this problem and for having articulated it in the clearest way:

> The prevalent assumption seems to be that if something is a unit of selection […], it must *therefore* be an individual. […] Unfortunately, we fail to see a compelling reason for such a

> connection. We do not see, particularly, why the fact that a population, a group or a species being a unit of selection would imply that it must be an individual. *The unity of a unit of selection need not be of the kind that is typical of an individual.* […] So it seems to us that the defenders of the Unity of Selection View of Biological Individuality have to establish *independently* that nothing can be a unit of selection if it is not a genuine individual—and we are not sure that there is a proof of that general thesis. (Chauvier 2017:4; emphasis modified)

Should we continue to treat individuality as a necessary condition for an entity to participate in the process of natural selection, or can selection operate on entities that do not qualify as individuals or do so only marginally?

To tackle this question, however, it is necessary to begin by carefully delineating the kind of entities that have been postulated as participants in the process of natural selection. Broadly speaking, scholars talk about two types of such entities: *units of selection* and *evolutionary (*or *Darwinian*) *individuals*. It is widely acknowledged that there is a "close association between the notions of biological individual and 'unit of selection', from Hull's work onwards" (Okasha 2023:13), although there is an ongoing confusion about how exactly these notions are related (Martens 2010:375). Importantly, the confusion is not merely semantic—although the polysemic character of these terms undoubtedly contributes to it. These concepts are at the core of two vast literatures that are united by their interest in characterizing the entities that participate in natural selection, while remaining largely independent from each other. For instance, the debate on the units of selection is rarely concerned with individuality (*pace* Hull), whereas the debate on evolutionary individuality mostly revolves around the relationship between this and other (non-evolutionary) kinds of biological individuality, while often ignoring that an entity might perform different functions in the process of evolution by natural selection. Through a plain and straightforward exposition, this review helps to clarify how these literatures, often treated in isolation, are in fact related.

Lastly, we require a working definition of 'individuality' before evaluating to what extent individuality is necessary for something to be a unit of selection or evolutionary individual. It is important to remark that, contrary to what Samir Okasha (2023) has claimed, 'individual' is regarded by most authors in these debates, from Hull onwards, as a substantive concept that signposts something different than the term 'unit,' and is not merely an idle label for 'entity,' 'thing,' or 'object'—otherwise, there would be no fact of the matter about its relationship to natural selection.

The aims of this review are thus threefold. (i) I will assess in a systematic way and for the first time whether the Individuality Assumption is warranted, by examining each of the main kinds of units of selection and evolutionary individuals that have been proposed. (ii) I will clarify the relationship between the concepts of units of selection and evolutionary individuals, as well as their respective literatures. This task has partially been undertaken before, most notably by Javier Suárez and Elisabeth A. Lloyd in their illuminating *Units of Selection* book (2023), on which I will heavily draw. However, Suárez and Lloyd focus almost entirely on the functional roles played by the units of selection and do not address individuality, which is the central concern of this article. (iii) I will connect the notions of units of selection and evolutionary individuality with the broader idea of individuality, particularly in the context of ETI. This might seem rather strange: isn't individuality the very focus of the literatures on evolutionary individuality and ETI? Appearances to the contrary, "evolutionary individuality" and "evolutionary transitions in individuality" aren't really about *individuality*, but about *evolvability* (for a recent overview of evolvability, see Pélabon et al. 2025). As I will argue, individuality and evolvability are indeed intimately related, but not as straightforwardly as to treat them as synonyms.

I provide a Glossary at the end of the article that succinctly defines and disambiguates the main concepts used throughout.

PRELIMINARIES

Let me begin with some preliminary remarks on the meanings of *units of selection*, *evolutionary individuality*, and *individuality* more broadly. Beyond laying the groundwork for the remainder of the review, this section begins to clarify how the literatures on the units of selection and on evolutionary individuality are connected. However, readers already well acquainted with the debates on units of selection and evolutionary individuality may skip the corresponding subsections and jump straight to the subsection 'Individuality.'

UNITS OF SELECTION

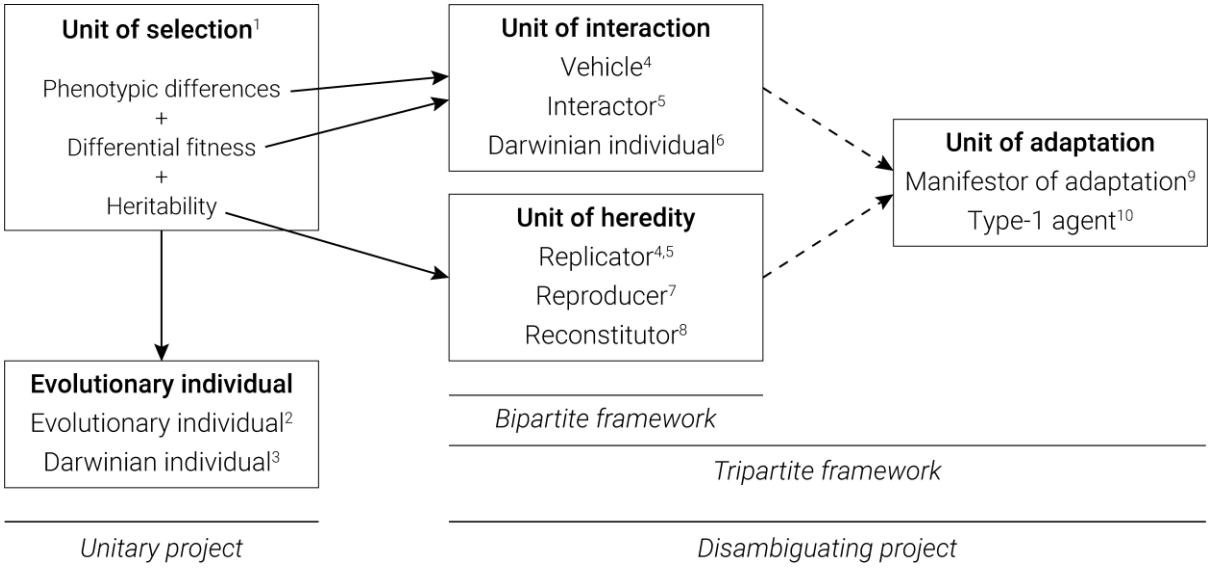
The literature on the units of selection is substantially larger and more complicated than the literature on evolutionary individuality, and in some sense it contains it. In this section, I adopt the framework developed by Suárez and Lloyd (2023) to offer an overview of the main types of units of selection that have been proposed.

The *locus classicus* in discussions about the units of selection is Richard C. Lewontin's (1970) "recipe approach." He explained that natural selection ensues whenever the following three conditions are met:

1. Different individuals in a population have different morphologies, physiologies, and behaviors (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). (Lewontin 1970:1; for discussion, see Godfrey-Smith 2007)

168 According to Lewontin, every entity that *simultaneously* possesses the three properties listed
169 above—phenotypic variation, differential fitness, and heritable variation in fitness—qualifies
170 as a *unit of selection*.

171 However, Suárez and Lloyd (2023) rightfully insist that one needs to be very careful when
172 talking about units of selection. Following Lewontin, some authors use the term to denote a
173 single type of entity, whereas others use it as a generic term that encompasses different types
174 of units defined by each of the functional roles contained in Lewontin's recipe. Suárez and
175 Lloyd call these two approaches "unitary project" and "disambiguating project," respectively
176 (for the rest of this section, I refer the reader to Figure 1).



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178 FIGURE 1. TYPES OF UNITS OF SELECTION (AFTER SUÁREZ AND LLOYD 2023). *Left-hand side:*
179 Lewontin's classic formulation of natural selection sets three conditions that an entity must meet in
180 order to qualify as a *unit of selection*. Recent approaches replace Lewontin's unit of selection with an
181 *evolutionary/Darwinian individual*. These, together with Lewontin's approach, are versions of the
182 "unitary project," which acknowledges only one type of unit of selection. *Right-hand side:* The
183 "disambiguating project" recognizes two ("bipartite framework") or three ("tripartite framework")
184 types of units of selection characterized by different functional roles within the process of natural

selection. The *vehicle*/*interactor*/*Darwinian individual* is the unit that directly interacts with the environment in such a way that its differential fitness—which is systematically connected to its phenotypic differences—causes differential replication or reproduction. The *replicator*/*reproducer*/*reconstitutor* is the unit that accounts for the process of heredity of fitness differences. The vehicle/interactor/Darwinian individual captures the first two conditions outlined by Lewontin, whereas the replicator/reproducer/reconstitutor captures the third. Finally, the *manifestor of adaptation*/*type-1 agent* is the unit that bears trans-temporally accumulated adaptations that may emerge as the result of the iteration of the process of selection across generations. Key references: [1]Lewontin (1970); [2]Clarke (2013); [3]Godfrey-Smith (2009); [4]Dawkins (1976); [5]Hull (1980); [6]Gould and Lloyd (1999); [7]Griesemer (2000b); [8]Veigl et al. (2022); [9]Lloyd (1992); [10]Okasha (2018).

According to the disambiguating project, a given object can play more than one role simultaneously and thus be more than one type of unit of selection at a time, but this need not be the case. In *The Selfish Gene*, Richard Dawkins (1976) split Lewontin's unit of selection into two functional roles abstracted from the roles of genes and organisms to reflect the genotype/phenotype distinction: the *replicator* and the *vehicle*. Shortly after, Hull (1980) reworked this framework and renamed the vehicle as *interactor*—and the concept of vehicle/interactor was later rebranded by Stephen J. Gould and Lloyd (1999, Gould 2002) as *Darwinian individual*. In a nutshell, the replicator is the unit in charge of the inheritance of variation (Lewontin's third condition), whereas the vehicle/interactor/Darwinian individual is the unit that shows phenotypic variation and has differential fitness due to its direct interaction with the environment (first and second conditions). In terms of replicators and interactors, natural selection is understood as "a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produce them" (Hull 1980:318; see also 1988a, Dawkins 1982a).

Not only the concept of vehicle but also that of replicator has been under scrutiny (see, e.g., Godfrey-Smith 2000, Griffiths and Gray 1997, Sterelny et al. 1996), and some authors have argued that it might be a special case of a more encompassing unit of heredity. For instance, James Griesemer (2000b, 2000a, 2000c, 2018) propose the concept of *reproducer* as a unit that accounts for heredity through material overlap. There are passages in Griesemer's works that suggest that the reproducer is not just *a* unit of selection—i.e., a generalized replicator, so to speak—but *the* unit of selection (e.g., Griesemer 2018:153). Here, however, I follow Suárez and Lloyd (2023, see also Veigl et al. 2022) in interpreting the reproducer as a generalization of the replicator and thus as part of the disambiguating project.

Both the replicator and the reproducer were conceived to explain the stability of traits across generations (i.e., Lewontin's third condition). The basic idea is that a trait reappears in the next generation due to units that transmit across generations the capacity to reconstruct the trait, either by coding the information to reconstruct the trait (i.e., replicators) or by transmitting some structured material that serves as the starting point for the reconstruction of the trait (i.e., reproducers), or both. In these perspectives, the transmission of information or material that guarantees the stability of traits across generations is inextricably linked to the formation of parent-offspring lineages.

However, a number of authors have recently argued that reproduction with lineage formation is not necessary for the trans-generational stability of traits, and thus for the process of evolution by natural selection to occur (see, e.g., Bouchard 2014, Bourrat 2015b, Charbonneau 2014, Nanay 2011, O'Malley 2016, Papale 2021). For instance, the 'it's the song, not the singer' account (Doolittle and Booth 2017, Doolittle and Inkpen 2018) postulates that certain interaction patterns (the "songs") can be re-created in each generation without lineage formation by the coming together of lineage-forming organisms (the "singers"). Instead, in the 'it's the song and the singer' (Bapteste and Papale 2021) account, the "singers" are simply

components of "songs" (i.e., they can themselves be "songs") and not necessarily organisms. More recently, Sophie J. Veigl et al. (2022) advanced the concept of the *reconstitutor* as the unit that gets recreated in each generation without the need for replication or material overlap.

The Dawkins-Hull approach is an example of the "bipartite framework" (Suárez and Lloyd 2023) that recognizes two functional roles or kinds of units of selection that can be collectively called *units of heredity*—replicator, reproducer, and reconstitutor—and *units of interaction*—vehicle, interactor, and Darwinian individual. However, Lloyd (1992, 1994, 2001, 2017) has long been arguing that there is more to the units-of-selection debates than can be captured by the Dawkins-Hull bipartite framework and its subsequent add-ons. Specifically, she has advocated for its extension into a "tripartite framework" that recognizes a third functional role besides the replicator and interactor: the *manifestor of adaptation*. This unit accounts for the accumulation of adaptations as a result of the continuous action of natural selection over time. A special case of manifestor of adaptation is Okasha's (2018) *type-1 agent*, which is defined as the unit in which many adaptive traits converge and synergistically contribute to a single overall goal (in contrast to type-2 agency, which consists in attributing agency to the process of evolution itself). We can refer to the manifestor of adaptation and type-1 agent collectively as *units of adaptation*.

Unlike the disambiguation project, the "unitary project" postulates the existence of a single type of unit of selection that simultaneously fulfils Lewontin's (1970) three criteria. Lewontin's concept of *unit of selection* is part of the unitary project, and more recent proposals rework it as *evolutionary* or *Darwinian individuals* (the latter should not be confused with Gould and Lloyd's Darwinian individual, which is an interactor and thus part of the disambiguating project). This is the sense in which the debates on the units of selection can be thought to include the literature on evolutionary individuality. However, this literature has developed to

some extent independently from the discussions on the units of selection, and thus I postpone its treatment until the next section.

Before moving on, it is worth underscoring that 'unit of selection' should not be taken to refer to a single, homogeneous concept. Instead, there is in principle a plurality of types of level- and, to some extent, substrate-neutral units of selection. This is important because it immediately suggests that individuality might be *necessary only for some types* of units of selection but not for others, or it might be *necessary in different ways or to different degrees* for different types of units of selection.

EVOLUTIONARY INDIVIDUALITY

The germ of the notion of an evolutionary individual can be traced back at least to Thomas H. Huxley's (1852) discussion on animal individuality. He proposed that an individual is the total developmental result of a fertilized ovum, no matter how much it changes during its ontogeny. Daniel H. Janzen (1977) labelled this concept *evolutionary individual*—the term had been used before in passing (e.g., by Hull 1975) but Janzen appears to have first endowed it with a technical meaning. Janzen argued that in species with asexual reproduction (e.g., parthenogenetic aphids), all the clones produced asexually between events of sexual reproduction (e.g., the whole population of aphids) constitute a single, scattered evolutionary individual. However, John L. Harper (1977) and Dawkins (1982b) pointed out that the relevant evolutionary unit (the 'genet') is defined by a 'bottleneck' stage (i.e., a substantial narrowing of material, sometimes down to a single or a few cells), irrespective of whether the bottleneck occurs during sexual or asexual reproduction.

Huxley-Janzen's individual and Harper-Dawkins's genet are *evolutionary* individuals in the sense that they are the developmental products that follow events of sexual reproduction (in the former) or bottlenecks more generally (in the latter), and thus their parts are genetically homogeneous and lack heritable variation in fitness. This is not entirely true in reality, however,

but this need not concern us here (for discussion, see especially Clarke 2011, 2012). The important point for our purposes is that these early proposals have certain features that characterize the idea of evolutionary individuality to this day.

First, as Suárez and Lloyd (2023) explain, evolutionary individuality is framed within the unitary project about the units of selection. Something is an evolutionary individual—to some degree—or it is not, and there aren't different types of evolutionary individuals tailored to different functional roles within the process of selection. Evolutionary individuals are, so to speak, units of heredity, interaction, and adaptation *simultaneously*. Interestingly, however, different accounts of evolutionary individuality slightly emphasize one of these roles over the others. For instance, Ellen Clarke's (2013) "evolutionary individuals" are primarily units of interaction (as the author herself notices in Clarke 2025:85), Peter Godfrey-Smith's (2009) "Darwinian individuals" are chiefly units of heredity, and Henri J. Folse III and Joan Roughgarden's (2010) "organisms" are principally units of adaptation.

Second, unlike how the units of selection are typically defined, evolutionary individuality is customarily defined in terms of certain properties or mechanisms by virtue of which the individual functions as a unit in the process of natural selection. Lewontin's abstract conditions for natural selection are thus in the background of more concrete material realizations that are taken as defining criteria for evolutionary individuality. For instance, the properties identified by Huxley-Janzen (sexual reproduction with germ-soma separation) and Harper-Dawkins (bottleneck) are such that they guarantee that a unit possessing them will necessarily act as a unit of selection according to Lewontin's schema. More recent accounts of evolutionary individuality refurbish these properties or abstract from them more general types or families of mechanisms that are used as criteria for evolutionary individuality. Thus, generalized notions of germ-soma separation and bottleneck are two of the three parameters with which Godfrey-Smith (2009) characterizes his own version of the evolutionary individual, and they are also

considered particular instances of ‘policing mechanisms’ in Clarke’s (2013) definition of an evolutionary individual (more on these accounts later).

Third, although it might sound obvious, individuality is more relevant for the notion of an evolutionary individual than it is for the notion of a unit of selection, and it has been so since the beginning. Janzen’s motivation for calling its evolutionary unit an ‘individual’ was to highlight the tension between “real” individuals in the biological world and our intuitive understanding of what an individual is. In more recent accounts, individuality figures more prominently in the problem agenda of evolutionary individuality than in the units of selection debates. Some typical questions in the literature on evolutionary individuality, which are seldom asked in the literature on the units of selection, are: How does individuality evolve? Why do some biological entities resemble “paradigmatic” individuals whereas others look more like groups?

This ties the literature on evolutionary individuality to the topics of multilevel selection and ETI (e.g., Clarke 2014, 2025, Folse III and Roughgarden 2010, Godfrey-Smith 2011, Helanterä and Uller 2019, Michod 2005). Here, the evolutionary unit is typically regarded as a “cohesive” evolutionary individual that is “simultaneously an interactor, reproducer, and manifestor/type-1 agent.” A transition then consists in the sequestration of reproduction and export of fitness from “objects in the lower level that once fulfilled the three roles, but do not embody them anymore” or embody them to lower degrees (Suárez and Lloyd 2023:58). When the locus of fitness shifts to the higher level after the transition, the individual might accumulate further adaptations, which would eventually give rise to complex adaptive phenotypes bringing the individual closer to the “paradigmatic” individuality characteristic of organisms (Buss 1987, Folse III and Roughgarden 2010, Pepper and Herron 2008, Queller and Strassmann 2009).

Other questions that are commonly asked in the literature on evolutionary individuality have to do with how evolutionary individuality relates to other kinds of biological individuality. The consensus view nowadays is that there is a plurality of legitimate, partially-overlapping kinds of biological individuals, each tailored to specific domains, perspectives, or theories (e.g., Wilson 1999, Godfrey-Smith 2013, Pradeu 2016, O'Malley 2021, Wilson and Barker 2024, McConwell 2023, Clarke 2025). In particular, most scholars conceptualize evolutionary individuality as one of main kinds of biological individuality alongside 'physiological' individuality (Figure 2). While evolutionary individuality constructs individuals in terms of their function in the process of evolution by natural selection, physiological individuality is closer to the notion of 'organism' (see especially Prieto 2023) in that it defines individuals as cohesive wholes characterized by persistence (Smith 2017), immunology (Pradeu 2010), metabolism (Dupré and O'Malley 2009), functional integration (Militello 2025), top-down regulation (Bich 2023), autonomy (Arnellos 2018), or agency (Fulda 2023).

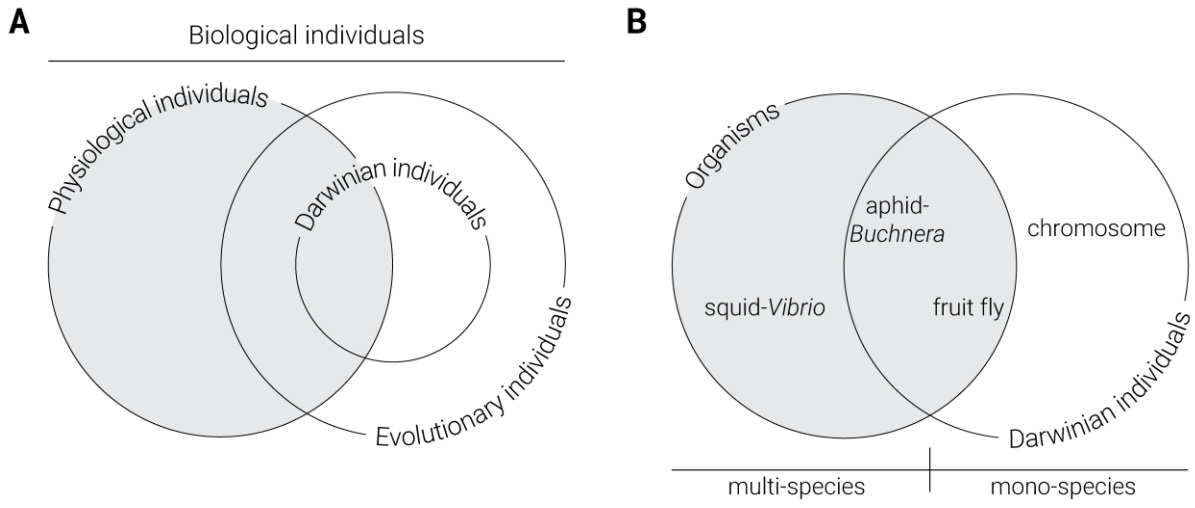


FIGURE 2. EVOLUTIONARY INDIVIDUALITY AS A KIND OF BIOLOGICAL INDIVIDUALITY. (A) Thomas Pradeu's (2016:811) diagram (redrawn with modifications) shows physiological individuals and evolutionary individuals as subcategories of biological individuals. (B) Similarly, Godfrey-Smith's

(2013:30) diagram (redrawn) subdivides biological individuals into organisms and Darwinian individuals and introduces a distinction between multi-species and mono-species individuals. In each diagram, shaded areas indicate organisms.

Although there are several accounts of evolutionary individuality (e.g., Buss 1987, Ereshefsky and Pedroso 2015, Folse III and Roughgarden 2010, Gardner and Grafen 2009, Goodnight 2013, Queller and Strassmann 2009), here I will focus on the two most influential and representative: Clarke's (2013, 2014, 2016a, 2021, 2025), which defines an *evolutionary individual* as a unit that possesses individuating mechanisms that ground its capacity to respond to natural selection, and Godfrey-Smith's (2009, 2011, 2013), which defines a *Darwinian individual* as a member of a population that meets Lewontin's conditions of variability, differences in reproductive success, and heredity.

Having treated the concepts of units of selection and evolutionary individuality, I now move on to offer a brief account of what 'individuality' means, and how we will use it when assessing the individuality of each of the units of selection in the remainder of this review.

INDIVIDUALITY

When asking whether an entity needs to be an individual in order to participate in the process of natural selection, we need a rough-and-ready definition of 'individual' that is adequate for our purposes. This should set individuals apart from universals such as 'reproduction' and from uncountable or massive objects such as 'tissue.' Also, we are interested in evaluating whether entities are individuals by virtue of their own constitutive or intrinsic properties and not merely individuated by *us*—that is, we are after an *ontological* concept of individual. Thus, we need the concept to rule out mere parts of individuals (such as animal tails or the pseudopodia of amoebas) or mere aggregates of individuals (such as a collection of animals in a zoo). The concept should also be abstract enough so that it can be applied to a

variety of biological entities from genes to ecosystems. Finally, it should reflect the intuitions behind the discussions on individuality in the context of the units of selection and evolutionary individuality rather than being artificially imposed from the outside.

I submit that a concept that satisfies all these requirements is that of a *metaphysical individual*. Without going into much detail (for a more detailed but still highly accessible treatment, see chapter 2 in Clarke 2025; for a more technical treatment, see Chauvier 2016, 2017), this concept characterizes an individual in terms of three properties: unity, identity, and autonomy.

i. *Unity* refers to the way an object's parts are coherently held together to form a single entity, and it involves two key aspects: *cohesion* and *spatial boundary*. Cohesion provides the "glue" that makes the parts of an individual function together as one, whereas the spatial boundary—physical, functional, or otherwise—determines what counts as part of the individual and what does not. In short, an individual is unified when it has a spatial boundary and a glue that integrates its parts into a single, coherent whole.

ii. *Identity* concerns the persistence and distinctness of an entity across space and time. It defines the conditions that separate one thing from others—synchronic identity—and the conditions under which something remains the same individual despite change—diachronic identity. In essence, identity establishes the criteria that allow an object to be recognized as distinct from others and as one and the same entity throughout its existence.

iii. *Autonomy* refers to an object's capacity to exist and persist on its own, rather than being wholly dependent on something else for its being. An autonomous entity is self-subsisting—it has its own mode of existence rather than existing merely as a part or aspect of another entity. However, autonomy does not imply total independence or

isolation, since even self-sustaining individuals depend on environmental conditions to maintain their existence.

Before we continue, three important caveats are due at this point. First, individuality is often conceptualized as an intrinsic property, but individuals do not live in a vacuum and thus their individuality depends to some extent on the external conditions they encounter (see Holzapfel 2024). However, I will abstract the environment away and focus on degrees of individuality as if the environmental variables were fixed.

Second, some scholars (e.g., Clarke 2025, DiFrisco 2019, Okasha 2023) think that a metaphysical concept of an individual cannot have shades—that something is an individual or it is not, and cannot have more or less individuality. But, at least intuitively, it seems perfectly fine to claim that, say, a pack of wolves has less individuality than a wolf. These authors would reply that both the pack of wolves and the wolf are metaphysical individuals—period—and that the difference we perceive between them is not in their metaphysical status but in the relative extent to which they belong to a certain category (e.g., 'physiological individuals,' 'evolutionary individuals,' etc.; DiFrisco 2019:850) or how much they approach the notion of a paradigmatic individual (Clarke 2025:146) or an organism (Okasha 2023:22). However, as Chauvier (2016:30–31, 43) argues, if individuality is defined *in terms of* properties like unity, identity, and autonomy (as here and in Clarke 2025), and these come in degrees, then individuality *must also* come in degrees. Thus, I do not see principled reasons to reject the idea that biological entities—and entities in general—can have different degrees of metaphysical individuality.

Third, I do not claim that the concept of an individual adopted here is the only one or even the best available. The important point is to have *some* metaphysical concept of an individual. Asking whether certain entity is an individual, whether it is more or less of an individual than another entity, or whether something counts as a criterion of individuality would be

meaningless without at least a provisional understanding of what 'individual' and 'individuality' mean.

Another reason for adopting this concept is that it meets our requirements. Firstly, the criterion of *identity* implies that individuals are particular entities in space and time, which means that the concept demarcates individuals from universals. Likewise, the criterion of *unity* means that individuals are cohesive and spatially bounded objects, and thus the concept demarcates individuals from massive objects. Additionally, the criterion of *autonomy* implies that individuals have a being of their own and not merely as parts or collections of other entities, which distinguishes them from mere parts and aggregates.

The concept also captures the right level of abstraction because it is sufficiently flexible to be used to assess a variety of biological candidates from genes and chromosomes to ecosystems and species. Each property—unity, identity, and autonomy—is materially realized differently depending on the specific case (Chauvier 2017). For instance, the unity of a gene is likely defined by the cohesion provided by the chemical bonds in the DNA molecule and the boundaries set by the gene's function, whereas the unity of a cell is defined by its spatial boundaries drawn by its membrane and the cohesion provided by its biochemistry. But interpreting these properties in concrete terms carries the risk of doing so too freely or loosely. The approach I will take minimizes this risk by keeping the analysis at a general, conceptual level. Instead of asking whether genes or cells are individuals, I will ask whether individuality is necessary for something to fulfil the functional roles attached to the notions of units of selection and evolutionary individuals *in abstracto*, while occasionally drawing on concrete examples for illustration.

Lastly, this definition of an individual captures and formalizes the way in which scholars across the literatures on evolutionary individuality and the units of selection have themselves described the general notion of individuality they were relying on. For example, Elliott Sober

448 (1991:294) underscored individuality through "the tight integration and interdependence of the
449 parts of a whole," which is captured by the criterion of autonomy. Hull described individuals
450 as "spatiotemporally localized cohesive and continuous entities" (Hull 1978:336)—which
451 corresponds to the criterion of unity—with "reasonably sharp beginnings and endings in time"
452 (Hull 1980:313)—which is covered by the criterion of identity. Similarly, Bernabé Santelices
453 (1999:152) understood an individual as a "well integrated and localized entity" (autonomy and
454 unity) "with reasonably well delimited boundaries in space and time" (identity). Additionally,
455 Gould (2002:602–603) defined the individual as having the ability to "maintain clear and
456 coherent boundaries during its lifetime" with "material continuity throughout" (identity), and
457 required that "the parts of an individual will work together so that the individual functions in a
458 distinctive and cohesive way" (unity and autonomy). These examples illustrate that whenever
459 scholars feel compelled to make explicit the underlying notion of individuality that subtends
460 the discussions on units of selection and evolutionary individuality, they list properties that are
461 captured by the metaphysical concept of an individual adopted here.

462 Therefore, we have a concept of an individual that we can confidently use to assess
463 whether and to what degree individuality—in terms of unity, identity, and autonomy—is
464 entailed by each of the main concepts of units of selection and evolutionary individuals that
465 have been proposed. From now on, whenever I use the terms 'individual' or 'individuality,' I
466 will do it in the metaphysical sense outlined above.

467 INDIVIDUALITY AND THE UNITS OF HEREDITY

468 In this section, I will assess whether the Individuality Assumption holds for the main units
469 of selection that have been postulated to account for the processes of inheritance, namely, the
470 *replicator*, the *reproducer*, and the *reconstitutor*. Then, in the next three sections, I will cover
471 the remaining types of units of selection and evolutionary individuals. The analysis will be

systematic and comprehensive, and therefore *lengthy*. Impatient readers may skip these four sections and turn directly to the section titled 'Challenging the Individuality Assumption,' where the results are wrapped up and discussed.

REPLICATOR

Dawkins famously depicts replicators as purposeful individuals that self-replicate and are responsible for the creation of the vehicles or interactors that house them, either directly or by providing the instructions for building them. However, he defines the replicator as "[a]ny entity in the universe of which copies are made" (Dawkins 1982b:293), and points out that the prime example of replicators is genes, which are stretches of DNA whose boundaries are rather fuzzy. In Dawkins words, "[a] replicator worthy of its name […] is not a discrete, all or none, unit at all, but a segment of chromosome whose length is determined by the strength of the 'whole animal level' selection pressure of interest" (Dawkins 1982a:49).

Similarly, Hull defined the replicator in similar terms as "an entity that passes on its structure directly in replication" (Hull 1980:318; see also 1988a). Although for Dawkins the "unity" of the replicator has little to do with individuality, Hull's position on this matter was more ambivalent. Sometimes, he insinuated that replicators are individuals (e.g., Hull 1992:186), and explained that spatiotemporal continuity is required for the process of replication (Hull 1978:341). However, he also pointed out that the kind of unity that replicators must have is structural rather than functional—i.e., a structure that can be passed on to the next generation with relatively high fidelity (Hull 1980:321). It is also worth noticing that Hull regarded entities other than genes or fragments of DNA as candidates for the role of replicators, as when he wrote that replication occurs "usually at the level of the genetic material, sometimes at the level of organisms and possibly colonies, but rarely higher" (Hull 1980:324; see also Sterelny et al. 1996).

Are replicators individuals in the sense outlined above? As both Dawkins and Hull remarked, the function of a replicator does not depend on its being a cohesive entity or having clear-cut spatial boundaries. What matters is simply that the replicator possesses a structure that can be copied and transmitted; in this sense, a replicator can in principle be a rather passive part of another entity. Thus, the role of a replicator is neither related to *unity* nor *autonomy*. However, *identity* does seem crucial for replicators, both synchronically and diachronically. This is because what defines a replicator is its "book-keeping" capacity, which depends on the specificity of its structural information and the preservation of this information through time. Thus, the specificity and persistence of its structural motif is what grounds the replicator's identity.

REPRODUCER

Griesemer (2000a, 2000b, 2014a, 2018) advanced the concept of a *reproducer* as a unit that passes on to its progeny the material basis and developmental mechanisms needed for further reproduction. Unlike the concept of replicator, the reproducer requires both development and material overlap. Griesemer calls 'development' the series of transformations that an entity undergoes to acquire the capacity to produce another entity, whereas material overlap means that "at least some material parts of the 'offspring' were formerly material parts of the 'parents'" (Griesemer 2018:154).

The requirements of development and material overlap impose a rather demanding restriction on the kind of entities that can qualify as reproducers. Godfrey-Smith (2009:81–84) points out that 'scaffolding reproducers' such as genes (more on this concept later) do not qualify as reproducers because their reproduction neither involves material overlap between "parent" and "offspring" nor confers the "offspring" the capacity to develop, for they lack development to begin with. In response, Griesemer argues that at least some scaffolding reproducers (e.g., retroviruses; Griesemer 2014b) do reproduce with material overlap and do

develop. To this, Godfrey-Smith would likely reply that "[m]aybe viruses 'develop,' but it is pushing the concept pretty hard to say so" (Godfrey-Smith 2009:84).

Without going into details about the precise limits of development and material overlap (for a deep dive, see Bourrat 2025a), it seems that the role of reproducer requires a higher degree of individuality than the replicator. These units likely require a similar degree of *identity*. However, the reproducer differs from the replicator in that it requires at least some *autonomy*, especially in the sense of "reproductive autonomy" (*sensu* Bourrat 2025a): whereas a replicator may be reproduced as a mere part of another entity, a reproducer always reproduces "by itself." The condition of *unity* is harder to determine in this case. On one hand, there seems to be no reason *a priori* why an entity with low cohesion and fuzzy boundaries would not be able to develop—i.e., undergo a series of transformations—and transmit its traits through material overlap. On the other hand, reproducers seem to demand a form of functional unity that sustains their capacity for autonomous reproduction.

To sum up, I think it is safe to conclude that the reproducer requires some degree of individuality. Specifically, it requires a high degree of identity, and a modicum of autonomy and unity.

RECONSTITUTOR

Veigl et al.'s (2022) concept of *reconstitutor* was devised as an extension of the replicator/reproducer to capture the transgenerational recreation of phenotypes or phenotypic traits without replication or reproduction at the focal level at which the phenotype or phenotypic trait is recreated. Specifically, the reconstitutor is defined as follows:

> The structure resulting from a set of relationships between different elements or processes that are actively involved in the recreation of a specific phenotypic variant in each generation

> regardless of the biomolecular basis of the elements or whether they stand in a continuous line of ancestry. (Veigl et al. 2022:16)

Notice that the role of the reconstitutor "is not confined to specific levels or scales and applies up and down the biological hierarchy" (Veigl et al. 2022:19). A prime example of reconstitutor is a holobiont that does not reproduce as a unit but reassembles in each generation, like cases in which a multicellular host horizontally acquires its microbiome from the environment (e.g., see Chiu and Gilbert 2015, Suárez 2020). It has been argued that these units are genuine individuals or even organisms, since they show a high degree of integration and functional organization despite being multispecies assemblages (see, e.g., Catania et al. 2017, Dupré and O'Malley 2009). But other examples of reconstitutors seem to greatly depart from individuality. For instance, Veigl et al. (2022) regard as reconstitutors pools of small RNAs in the nematode *Caenorhabditis elegans* that are trans-generationally maintained in the absence of environmental triggers.

Taking all this into account, individuality does not appear to be a requirement for being a reconstitutor. In particular, reconstitutors need not be cohesive or spatially-bounded entities, and thus *unity* is not necessary for an entity to function as a reconstitutor. *Autonomy* is also contingent rather than constitutional, for a reconstitutor might be a part of a proper individual, a system of relations between individuals, or a mere recurrent pattern. And since the defining feature of a reconstitutor is the reliable recreation of a relational pattern and not its distinctness and persistence, *identity*—especially diachronic identity—seems to play no essential role either.

Individuality and the Units of Interaction

In this section, I will move on to assessing whether the Individuality Assumption holds for the units that are selected through their interaction with the environment. These units are

captured by the slightly different concepts of *vehicle*, *interactor*, and Gould and Lloyd's *Darwinian individual*.

VEHICLE

Dawkins defines the vehicle as "any *relatively discrete* entity, such as an individual organism, which houses replicators […] and which can be regarded as a machine programmed to preserve and propagate the replicators that ride inside it" (Dawkins 1982b:295; emphasis added). He also suggests that vehicles are individuals in the sense that we are using the term, that is, as "spatiotemporally localized, cohesive and continuous entities" (Dawkins 1982a:58). These can be as varied as chromosomes, groups of organisms, and community- or ecosystem-forming multispecies assemblages (Dawkins 1982a:50–51).

However, for Dawkins, the true units of selection are the replicators, which are selected through their phenotypic effects on vehicles. In this sense, individuality is rather contingent to vehicles. In Dawkins' words,

> vehicles often turn out to be the objects that we recognize as organisms, but this did not have to be so. *It is not part of the definition of a vehicle.* […] Darwinism can work on replicators whose phenotypic effects (interactors) are too diffuse, too multileveled, too incoherent to deserve the accolade of vehicle. (Dawkins 1994:617; emphasis added)

Clearly, the role of the vehicle not only dispenses with but also rules out *autonomy*: vehicles are epiphenomena of the replicators they contain and are fully controlled by them. And, as Dawkins explains, vehicles might be "diffuse" and "incoherent," and thus *unity* and *identity* and likely not required for them either. I will spell this out in more detail when discussing the interactor, but for now, it seems reasonable to conclude that although organisms and other highly individualized entities may be paradigmatic cases of vehicles, the functional role that vehicles represent in Dawkins' view is independent of their individuality.

593 In this section, I will treat Hull's interactor and Gould and Lloyd's Darwinian individual
594 together because they are essentially the same unit. Notice, however, that in their discussions
595 of the Darwinian individual, Gould and Lloyd included all three of Lewontin's conditions
596 among its attributes. These further requirements would turn the Darwinian individual into a
597 unit of selection *à la* Lewontin rather than just an interactor. In any case, I classify the
598 Darwinian individual as an interactor within the disambiguating project about the units of
599 selection because that is how it has been portrayed both by some of its proponents (Suárez and
600 Lloyd 2023:61) and detractors (Godfrey-Smith 2013:33).

601 Unlike Dawkins' vehicle, Hull's concept of an interactor includes an inbuilt degree of
602 individuality: an interactor is defined as "an entity that interacts as a *cohesive whole* with its
603 environment in such a way that this interaction causes replication to be differential" (Hull
604 1988b:408; emphasis modified). Thus, for Hull, an interactor must be sufficiently cohesive to
605 respond to the environment as a unit, and for its parts to be selected together as one and thus
606 share a common evolutionary fate. As in the case of vehicles, organisms are paradigmatic
607 interactors, but there are many other sorts of biological objects that can qualify as interactors
608 according to Hull, from genes and chromosomes to groups and perhaps even larger entities
609 (Hull 1978, 1980, 1988a, see also Brandon 1988).

610 However, the interactor's "cohesiveness" is related to individuality only in a very limited
611 sense. With some nuances (for an overview, see Suárez and Lloyd 2023:20–22), scholars
612 concur that the "cohesiveness" required for interactors is "customarily reduced merely to the
613 existence of some indirect genetic effects [e.g., epistasis] between the components of the
614 interactor" (Suárez and Lloyd 2023:24) that result in fitness alignment between the components
615 and emergent fitness at the level of the whole interactor (for a generalized account of interactors
616 without cohesion, see Papale and Doolittle 2024).

It could be argued that, even if individuality is not required for something to be an interactor, it is nevertheless an evolved feature that results from selection *at the level of* the interactor. However, this need not be the case either. First, selection processes at the level of the interactor "do not necessarily require, nor do they invariably produce, [the] functional organization or harmony of parts" (Gould and Lloyd 1999:11905) that is typical of an individual (Okasha 2018:53). Second, the interactor is by definition the unit at the level on which selection *acts*, but the *effects* of selection may accumulate at another level. Therefore, even if individuality was a product of selection at the level of the interactor, it could manifest at a different level. Elliot Sober made this point clearly:

> Selection at a given level of organization does not have to produce objects at that level that are highly individualistic. And an object at a given level may be highly individualistic even though it is not the result of selection at that level. (Sober 1991:294)

Now we can ask whether individuality is necessary for the interactor/Darwinian individual. According to Hull's definition and its subsequent expansions, an interactor can be a collective entity whose being is almost fully dependent on the being of its composing particles. In this sense, *autonomy* is not required for the interactor. Also, the interactor may be ephemeral or compositionally fluid, and thus *identity* is largely irrelevant to it. With respect to *unity*, the interactor does not require clearly defined boundaries but only a minimal degree of cohesion in the sense that the interacting particles in the collective mutually influence their fitness.

INDIVIDUALITY AND THE UNITS OF ADAPTATION

In this section, I shall deal with the Individuality Assumption with respect to the units that bear trans-generationally accumulated adaptations as the result of past selection: the *manifestor of adaptation* and the *type-1 agent*.

The concepts of vehicle and interactor were originally meant to capture the evolutionary role best represented by organisms and organism-like individuals. However, an interactor need not be "organismal" to fulfil its role, and the concept does not adequately account for the accumulation of adaptations, which has traditionally been regarded as a hallmark of individuality and organismality (for discussion, see the target article by Wilson and Sober 1994, and the replies to it in the same issue). An interactor usually shows "product-of-selection adaptations," this is, traits that are the result of selection at its level (e.g., industrial melanism in peppered-moths). But, strictly speaking, it need not show "engineering adaptations," namely, traits that seem engineered or tinkered (e.g., the beak's shape in Darwin's finches). Hereafter, I use 'adaptation' only in the latter sense (for further discussion on the distinction between these two meanings of the term adaptation, see Lloyd 2008).

The manifestor of adaptation was introduced to capture the accumulation of adaptations that (sometimes) results in functionally integrated units. Specifically, this concept is defined as

> an entity in the biological hierarchy that bears traits that make it look as if it were 'engineered' or tinkered to fit or respond to problems/challenges in its environment. These traits can be called *engineering* or *trans-temporally accumulated* adaptations, as they are traits that result from the cumulative transgenerational effect of natural selection acting at a specific level, showing a high degree of 'cohesiveness' or organization […]. (Suárez and Lloyd 2023:23–24)

The adaptations that this unit manifests are not necessarily the result of the direct interaction of the unit with the environment—this is, the manifestor of adaptation need not be an interactor. Also, the accumulation of adaptations does not necessarily indicate that selection is currently acting: it only indicates that selection *has acted* in the past, either at the focal level of the manifestor or at another level.

It is tempting to link individuality to the manifestor of adaptation because the trans-generationally accumulated engineering adaptations likely manifest in individualized bodies. The idea is that "since adaptations are usually considered adaptations *of an individual*, it is necessary to establish criteria to delineate the biological individuals that bear them before the identification of the adaptations becomes biologically feasible" (Suárez and Triviño 2020:1). Conversely, the presence of adaptations is often taken as an indication of individuality in collective entities. For instance, an "argument in favour of the claim that multispecies biofilms are evolutionary individuals is the phenomenon of higher-level adaptation," and "[n]obody who denies that biofilms are multicellular individuals is likely to accept that biofilms exhibit adaptations" (Clarke 2016b:202–203).

A problem with linking adaptations to individuality is that adaptations are not necessarily manifested in highly individualized entities, and thus we often do not know which entity—particles or collective—is the manifestor of a given adaptive trait. Consider the case of the honeybee's stinger. This structure likely evolved by natural selection as a modification of the ovipositor (Blaimer et al. 2023), and is used by honeybees to repel aggressors by piercing through their skin and injecting venom. Due to its barbed profile, the stinger usually remains firmly lodged to the aggressor's skin while autotomizing from the bee's body, which causes the death of the bee by disruption of its abdominal organs. Once detached from the bee, the stinger autonomously continues to penetrate the aggressor's skin, pump venom, and release alarm pheromones that attract and recruit other bees (Nouvian et al. 2016, Shorter and Rueppell 2012). The stinger can perform these functions because it is a highly complex structure that includes a piercing apparatus, pumping musculature, venom glands and sac, pheromone-producing glands, and a nervous ganglion that coordinates its behavior (Ramirez-Esquivel and Ravi 2023).

689 The stinger is clearly a sophisticated engineering adaptation, and, at least intuitively, one
690 could assume that the honeybee is the individual that manifests it—after all, a stinger is a part
691 of an individual bee! Yet, the fact that its use causes the death of its bearer makes its adaptive
692 value the object of diverging interpretations. A possible explanation from the perspective of
693 'kin selection' or 'inclusive fitness' is that, by defending the colony with the aid of its stinger,
694 the honeybee enhances the fitness of its relatives, who bear the same heritable trait. Therefore,
695 under this interpretation, each honeybee is the manifestor of adaptation. Alternatively, an
696 explanation within the 'multi-level selection' or 'group selection' frameworks is that the stinger
697 is harmful at the honeybee-level but adaptive at the colony-level, and thus the colony is the
698 manifestor of adaptation for this particular trait (e.g., Suárez and Triviño 2020).
699 The choice between these different evolutionary explanations has been the object of
700 intense debates in evolutionary biology (for an overview, see Birch 2017a). Generally speaking,
701 there is a *formal* equivalence between these two explanations of the honeybee stinger—and of
702 adaptations at large—that does not imply *causal* equivalence between them (Godfrey-Smith
703 and Kerr 2013, Okasha 2016). Since the manifestation of a given adaptive trait does not
704 necessarily occur in highly cohesive individuals, the resolution of this sort of conundrum in
705 favor of one or the other explanation customarily requires further causal information about the
706 entities at stake.
707 In sum, a manifestor could in principle be a rather loosely-integrated collective entity with
708 blurred boundaries, transient organization, and a being largely dependent on the particles that
709 compose it (e.g., think of collective adaptive behaviors in animal groups and structural
710 collective adaptations in entities like biofilms). However, it is reasonable to assume that the
711 accumulation of adaptations is linked to individuality, since engineering traits tend to be
712 strongly associated with cohesion, persistence, and functional integration. Therefore, I will

conclude rather conservatively that only relatively low degrees of *unity*, *identity*, and *autonomy* are required for an entity to manifest adaptations.

TYPE-1 AGENT

As pointed out above, the manifestation of a particular adaptation *per se* does not say much about the individuality of the manifestor. As Okasha (2018:58) explains, "[i]f we focus on a single pro-social trait [e.g., the honeybee's stinger], it may be possible to explain it in terms of either individual or group advantage, but the same need not be true of other traits." Instead, we should minimally expect individuals to be bundles of many adaptive traits working concertedly toward the individual's goals. This is the rationale behind Okasha's notion of type-1 agent, which "presupposes that the entity that is treated as an agent exhibits a 'unity-of-purpose,' in the sense that its evolved traits contribute to a *single* overall goal" (Okasha 2018:5).

The kind of unity that characterizes type-1 agents is likely proprietary of organisms and other highly individualized biological entities. Thus, unlike the other units of selection I have reviewed so far, the concept of type-1 agent seems to be tightly connected to high degrees of individuality. It should be noticed, however, that Okasha (2018:2) leaves the possibility open for entities such as genes to qualify as type-1 agents. In particular, he argues that genes must be treated as agents when their interests are not aligned with the interests of the organism that hosts them. This occurs in cases of 'intra-genomic conflict,' in which certain phenotypic traits related to the presence of "selfish" genetic elements are detrimental to the organism (see Gardner and Úbeda 2017).

Leaving aside this borderline case, type-1 agency presupposes a relatively high degree of individuality. To exhibit "unity of purpose," an entity's traits must work concertedly toward a common goal, which entails *unity* in the form of functional—and likely also structural—integration. Moreover, *identity*—the persistence and distinctness of the entity across time—subtends the maintenance and coordination of its goal-seeking activities. Some degree of

autonomy is also indispensable, since an entity would not have goals *of its own* if it was a mere part or aggregate.

This captures the fact that, when a collective of entities shows "high degree of cooperation and functional integration, we tend to elevate them to the status of 'individuals' and regard their members as parts of a single whole" (Okasha 2018:53). It also aligns with the idea that organisms are units of "near-unanimous design" (Queller and Strassmann 2009:3144), that is, *loci* of multiple adaptative traits that concertedly underpin their functional organization (Folse III and Roughgarden 2010, Gardner and Grafen 2009, Pepper and Herron 2008).

INDIVIDUALITY AND THE UNITARY PROJECT

In this section, I will focus on the Individuality Assumption in relation to the units into which the different functional roles of the units of selection are combined. I will start with Lewontin's *units of selection*, and then discuss Clarke's *evolutionary individuals* and Godfrey-Smith's *Darwinian individuals*.

LEWONTIN'S UNIT OF SELECTION

Although in his formulation of the process of natural selection Lewontin conceptualized the units of selection as "individuals in a population" that show phenotypic variability, differential fitness, and heredity, he also pointed out that "[t]he generality of the principles of natural selection means that *any entities in nature* that have variation, reproduction, and heritability may evolve" (Lewontin 1970:1; emphasis added). Thus, according to him, "the principles [of natural selection] can be applied equally to genes, organisms, populations, species, and at opposite ends of the scale, prebiotic molecules and ecosystems" (Lewontin 1970:2).

Clearly, Lewontin's units of selection do not presuppose individuality. His formulation of natural selection requires only that entities exhibit variation, differential fitness, and heritability—conditions that can be met by units at any hierarchical level, regardless of their degree of individuality. In fact, contrary to the idea that "ecosystems are not individuals [and therefore] cannot be units of selection" (Maynard Smith and Szathmáry 1995:7), recent scholarship on the evolution of ecological systems shows that natural selection can take place "without individuals." For instance, Sébastien Ibanez has recently argued that despite not meeting standard definitions of individuality, ecosystems can evolve by natural selection if they have phenotypes consisting of clusters of properties maintained by the causal interaction of different biological entities. Ibanez concludes:

> Units of selection [*sensu* Lewontin] do not require evolutionary individuality as soon as "causal influences responsible for similarity" is a sufficient criterion, and units of evolution are not necessarily cohesive individuals, since they are best understood as clusters of properties. (Ibanez 2020:103; see also Lenton et al. 2021)

CLARKE'S EVOLUTIONARY INDIVIDUAL

Clarke's account focuses on the mechanisms that grant an entity the capacity to undergo selection at its focal level. At the core of her approach is the idea that an 'evolutionary individual' is an entity at the level upon which selection is more likely to act and thus the most relevant unit to count for fitness assessments in evolutionary explanations and predictions.

Clarke's approach touches upon the core problem in the debates on group selection, namely, determining the level at which selection acts in situations where there are at least two levels of compositionally related entities—particles and collectives. Usually, this problem is approached empirically by measuring the variance in fitness at the level of the particles and the level of the collectives (e.g., by applying Price's multilevel covariance equation, inclusive

fitness analysis, or contextual analysis, among other methods; for discussion, see Okasha 2006, Birch 2017b). The occurrence of variance in fitness at the two levels is indicative that selection may be acting on both levels. Additionally, if differences are found between the variances, selection may be acting on one level relatively more than on the other.

However, it has been pointed out that the detection of fitness variance at one level can be a statistical artefact or an epiphenomenon of selection at another level—i.e., a "cross-level by-product" (Okasha 2006, for a recent overview, see Bourrat 2025b). Therefore, statistical methods must be supplemented with explanations in terms of plausible mechanisms that may cause the detected differences in fitness variance (notice that this situation is analogous to the problem of determining at which level an adaptation is manifested). Clarke calls these mechanisms *policing* and *demarcation mechanisms* and groups them under the banner of *individuating mechanisms*. In other words, "[a]n individuating mechanism is a mechanism that either limits an object's capacity to undergo within-object selection (policing kind) or increases its capacity to participate in between-object selection processes (demarcation kind)" (Clarke 2013:427).

Clarke's concept of individuating mechanisms generalizes the different accounts of evolutionary individuality we saw in the 'Preliminaries' section. For instance, the Huxley-Janzen criterion of *sex* is a concrete example of a demarcation mechanism that enhances between-collective selection by increasing variation among collectives, whereas the Harper-Dawkins criterion of *bottleneck* constitutes an example of a policing mechanism that reduces within-collective selection by minimizing the variation among the particles in the collective.

In Clarke's account, individuating mechanisms are central to the *evolutionary individual* because they concentrate selection at its level. Consequently, an evolutionary individual is "all and only those units of living matter that have a capacity to form lineages/populations that can evolve by natural selection, because of the action of Individuating Mechanisms" (Clarke

2025:104). Additionally, the identification of individuating mechanisms can be utilized to explain or predict instances of higher-level variance in fitness and thus mitigate the problem of cross-level by-products (Clarke 2016a).

How much of an individual is Clarke's evolutionary individual? To address this question, it is important to remark that Clarke's evolutionary individual is primarily a unit of interaction. As such, the evolutionary individual requires only a certain degree of cohesiveness so that selection concentrates at its focal level. The same can be said, *mutatis mutandis*, of its role as a unit of heredity, for which it only requires "[s]ome kind of growth, with a tendency to fragment on reaching a threshold size" (Clarke 2013:434, see also 2014:313–314) that confers on it "a capacity to form lineages/populations" (Clarke 2025:104).

What about the individuality of the evolutionary individual *qua* unit of adaptation? The individuating mechanisms that define the evolutionary individual can be quite rudimentary (e.g., at the beginning of an ETI; Clarke 2014). Still, the most common examples of individuating mechanisms (e.g., bottleneck, sex, germ-soma separation, immune system, etc.) are clear cases of trans-temporally accumulated engineering adaptations, which make evolutionary individuals manifestors of adaptation. As we saw earlier, however, the manifestation of a given adaptive trait does not necessarily occur in a cohesive individual. Clarke acknowledges this by pointing out that the definition of an evolutionary individual in terms of specific traits is "very much at odds with how we usually talk about organisms—we don't say that finches are organismal for beak depth" (Clarke 2025:153, see also 2017).

The issue is that even if Clarke's evolutionary individuals are manifestors of specific adaptive traits, this does not mean they are type-1 agents. Clarke argues that her individuating mechanisms "go some way to ameliorating this problem" because "[a] mechanism which prevents fitness differences between the parts of an object in respect of one trait will often prevent differences in respect of other traits at the same time" (Clarke 2016a:908). This aligns

834 with Okasha's view that minimization of within-collective conflict through the action of
835 policing mechanisms is a mark of type-1 agents:

836 > Recall the unity-of-purpose constraint: for a biological entity to be treated as an agent, its
837 > evolved traits [e.g., individuating mechanisms] must have complementary rather than
838 > antagonistic functions; otherwise the entity cannot sensibly be regarded as 'trying' to achieve
839 > a goal by means of its traits. This is a conceptual point; empirically, it requires the absence of
840 > internal conflict, and thus [policing] mechanisms for suppressing or minimizing conflict.
841 > (Okasha 2018:37)

842 However, I do not think that Clarke's evolutionary individuals need to be type-1 agents
843 and thus show a high degree of individuality. Individuating mechanisms can in principle be
844 only strong enough to guarantee that there is an interactor at the collective level, which does
845 not require the suppression of conflict at the particle level and unity of purpose at the collective
846 level. In fact, as Suárez and Lloyd have remarked,

847 > evolutionary change researchers […] have persistently shown that the presence of an
848 > interactor at the higher level [i.e., an evolutionary individual] may be feasible even if there is
849 > a high degree of competition and variation between the entities at the lower level. In fact, a
850 > high level of competition at the lower level [i.e., the lack of unity of purpose] does not
851 > necessarily preclude the efficacy of selection at the higher level. (Suárez and Lloyd 2023:34–
852 > 35, see also Patten et al. 2023)

853 A last point to notice is that there are many references in Clarke's work, including the very
854 definition of an evolutionary individual (Clarke 2025:104–105), to the fact that the concept is
855 restricted to *living* things. Moreover, Clarke makes clear that her approach presupposes simple
856 living individuals (e.g., cells) that compose the collective individuals she is concerned with
857 (Clarke 2013:432–435, 2014:304, 307). She further restricts the scope of the concept to
858 portions of living matter "[b]igger than organs, but smaller than populations" (Clarke

2016a:893) and takes viruses to fall outside it unless "we decide to consider them as alive" (Clarke 2021:116). As I see it, the restriction of evolutionary individuals to living beings is unwarranted, for there is no in-principle reason why the concept would only apply to living beings. In fact, Clarke admits that even genes can qualify as evolutionary individuals "on those occasions when they are selected separately from the rest of the genome, as in the case of meiotic driver genes" (Clarke 2021:116).

In sum, Clarke's evolutionary individual requires only a minimal degree of individuality—it need not display high levels of *unity*, *identity*, or *autonomy*, for its cohesion may be loose, its spatial boundaries fuzzy, its identity ephemeral, and its dependence on its constituent particles high, yet individuating mechanisms can still concentrate selection at its level. The individuality required by Clarke's evolutionary individuals is on a par with that required by interactors and replicators, or—if we focus on cases in which the individuating mechanisms are engineering adaptations—that of manifestors of adaptation.

GODFREY-SMITH'S DARWINIAN INDIVIDUAL

Godfrey-Smith's Darwinian individuals are "simultaneously interactors and reproducers, where their joint reproduction has been achieved by a process of accumulation of adaptations [i.e., manifestors/type-1 agents] with respect to the sequestration of reproduction at their level" (Suárez and Lloyd 2023:63). Thus, for assessing the individuality of Darwinian individuals, we could resort to the strategy of analyzing how individuality relates to each of its functional roles separately, as we did for the case of Clarke's evolutionary individuals. However, the individuality of Darwinian individuals can be addressed more directly due to the way Godfrey-Smith laid out the concept.

Godfrey-Smith (2009, 2015) regards reproduction as the formation of parent-offspring lineages whereby offspring resemble their parents, at least in a weak sense. He calls a population of causally interacting entities that reproduce a 'Darwinian population,' and each of

its members a 'Darwinian individual.' He also makes a distinction between three kinds of reproducing entities represented most clearly by genes and viruses, cells, and multicellular organisms: *scaffolded*, *simple*, and *collective* reproducers, respectively. Scaffolded reproducers are entities that do not reproduce by themselves but are reproduced by other entities or as the result of the reproduction of a larger entity they partake in. Instead, simple reproducers can reproduce independently, and collective reproducers reproduce as a whole while having parts that also have the capacity to reproduce.

Of the three types of reproducers, Godfrey-Smith pays special attention to collective reproducers, which he characterizes in terms of three features: *bottleneck* (*B*), *germ line* (*G*), and *integration* (*I*). Those entities that exhibit the highest degree of these three parameters are considered paradigmatic individuals that form Darwinian populations able to "produce novel and complex organisms, highly adapted to their circumstances" (Godfrey-Smith 2009:6). Instead, a low degree of these parameters is the mark of marginal Darwinian populations that can evolve by natural selection but are less able to produce high degrees of novelty, complexity, and adaptability.

The parameters *B* and *G* are concrete instances of individuating mechanisms *sensu* Clarke, and they also play these roles in Godfrey-Smith's account. The third parameter, *I*, "has more general importance" (Godfrey-Smith 2009:91) and is "a summary of such features as the extent of division of labor, the mutual dependence (loss of autonomy) of parts, and the maintenance of a boundary between a collective and what is outside it" (Godfrey-Smith 2009:93). Understood this way, it is clear that *I* does all the heavy lifting in determining the individuality of collective reproducers—in fact, *I* arguably *is* individuality. A low value of *I* is associated with "loose aggregations of entities capable of independent living," an intermediate value corresponds to "a level of integration seen in colonies and very simple organisms like sponges,"

908 and a high value is characteristic of "the level seen in complex multicellular organisms"
909 (Godfrey-Smith 2009:94).

910 Unlike *B* and *G*, which cannot be ascribed to things like genes and cells, *I* can also be used
911 to characterize the individuality of simple and scaffolded reproducers. Godfrey-Smith explains:

912 > A high value of *I* is almost inevitable in a simple reproducer, like a cell, and not needed in a
913 > scaffolded reproducer. Many scaffolded reproducers […] are special parts of the machinery
914 > of a simple reproducer (chromosomes), or enter into Darwinian processes via the machinery
915 > contained in other things (viruses). (Godfrey-Smith 2009:100)

916 In other words, simple and collective reproducers have at least some degree of
917 individuality, whereas scaffolded reproducers might not have individuality at all except in the
918 sense of identity (as in the replicator). Their lack of individuality notwithstanding, scaffolded
919 reproducers such as "[g]enes, chromosomes, and other fragments of organisms can all form
920 Darwinian populations," and thus they are Darwinian individuals (Godfrey-Smith 2009:85). In
921 sum, individuality is not essential to Darwinian individuals. As Godfrey-Smith acknowledges,
922 in his account, "[r]eproduction involves the creation of a new entity, and this will be a countable
923 individual. But the right sense of 'individual' to use here is a relaxed one:" all that matters is to
924 be able to tell "who came from whom, and roughly where one begins and another ends"
925 (Godfrey-Smith 2009:86).

926 ## CHALLENGING THE INDIVIDUALITY ASSUMPTION

927 Ever since the influential work of Hull, a conceptual link of necessity has been drawn
928 between individuality and natural selection. Many scholars in both the units-of-selection and
929 evolutionary-individuality literatures have accepted the Individuality Assumption—that for
930 something to qualify as a unit of selection, it must be an individual. Yet this claim has not been

subjected to systematic scrutiny until now. In this section, I will discuss the results of my analysis and propose a reconsideration of the relationship between individuality and selection.

THE SCOPE OF THE UNITS OF SELECTION

I have assessed the extent to which individuality is required for the main concepts of units of selection and evolutionary individuals that have been proposed in the literature: Dawkins and Hull's replicator, Griesemer's reproducer, Veigl et al.'s reconstitutor, Dawkins' vehicle, Hull's interactor, Gould and Lloyd's Darwinian individual, Lloyd's manifestor of adaptation, Okasha's type-1 agent, Lewontin's unit of selection, Clarke's evolutionary individual, and Godfrey-Smith's Darwinian individual. What general patterns can be extracted from this analysis?

As a starting point, it is instructive to inspect what types of biological entities fall within the scope of each of these concepts. Table 1 shows several types of entities, from genes to species, arranged from left to right according to the conventional order of the biological hierarchy. An immediate conclusion that can be extracted from inspecting the table is that a given kind of entity can serve different functional roles (Table 1, read vertically). Thus, for example, holobionts have been characterized as reproducers (e.g., Griesemer 2014b, Roughgarden et al. 2018), reconstitutors (e.g., Doolittle and Booth 2017, Suárez 2020, Veigl et al. 2022), interactors (e.g., Booth 2014, Gilbert et al. 2018, Suárez and Triviño 2019), manifestors of adaptation (e.g., Stencel and Wloch-Salamon 2022, Suárez and Triviño 2020), Darwinian individuals (e.g., Godfrey-Smith 2013, Martens 2021), or some combination thereof (see Lloyd 2018). Conversely, a given functional role can be fulfilled by very different kinds of entities (Table 1, read horizontally).

TABLE 1. SCOPE OF THE UNITS OF SELECTION CONCEPTS. Tick marks (✓) indicate the sorts of entities that have been proposed in the literature as examples of each unit of selection concept. Interrogation marks (?) indicate entities that could in principle fulfil a role but whose status is unclear or has not been discussed explicitly. See references in the text.

Units of selection	**Entities**									
	Genes	Chromosomes	Viruses	Cells	Organisms	Holobionts	Groups[a]	Demes	Ecological units	Species
Units of replication										
Replicator	✓	✓	✓	✓	✓		?			
Reproducer			?	✓	✓	✓[d]	?			
Reconstitutor	✓	?	?	?	?	✓	✓	?	✓	
Units of interaction										
Vehicle		✓	✓	✓	✓	✓[e]	✓	?	✓	?
Interactor		✓	✓	✓	✓	✓[e]	✓	?	?	✓
Gould and Lloyd's Darwinian individual	✓	✓	✓	✓	✓	✓[e]	✓	✓	?	✓
Units of adaptation										
Manifestor of adaptation	?	?	?	?	✓	✓	✓	?	?	?
Type-1 agent	✓[b]		?	?	✓	?	?			
Unitary project's units										
Lewontin's unit of selection	✓	✓	✓	✓	✓	✓[d]	✓	✓	✓	✓
Clarke's evolutionary individual	✓[b]		✓[c]	✓	✓	✓[e]	✓	?	?	?
Godfrey-Smith's Darwinian individual	✓	✓	✓	✓	✓	✓[d]	✓	?	?	✓

[a] Including superorganisms and colonial organisms. [b] Only in certain cases, such as when there is intra-genomic conflict. [c] If considered alive. [d] If reproduces as a unit. [e] If it is selected as a unit.

These patterns indicate that the particular properties of the entities are non-essential to their functioning in the process of evolution by natural selection. In other words, the types of functional roles in relation to natural selection are not determined by the specificities of their material realizations (see also Griesemer 2005:72–73). Moreover, some of these entities (e.g., genes, ecological units, species, and even holobionts) are not commonly regarded as individuals, or are considered individuals only in a marginal or loose sense. This already suggests that individuality might not be essential to an entity's role as a unit of selection. Let us now explore this conclusion in more detail.

THE INDIVIDUALITY SPACE

Let us now shift focus from the *extension* of the concepts of units of selection and evolutionary individuals—that is, the concrete types of entities to which they may apply—to their *intension*—that is, to what each concept of unit of selection requires in terms of individuality. For this aim, I propose a visual representation consisting of a three-dimensional space in the manner of Godfrey-Smith's (2009) "Darwinian space"—an 'Individuality Space,' if you will. The three dimensions that define the Individuality Space in our case correspond to the three properties that define (metaphysical) individuality—unity, identity, and autonomy. As discussed earlier, these properties are scalar, so we can represent them as taking any value from 0 to 1 along their corresponding axes (Figure 3).

We can then locate the different types of units of selection within the Individuality Space according to the minimal degree of each of the individuality-defining properties that is required for an entity to qualify as a unit of selection of each type—that is, according to the degree of individuality presupposed by the functional role defined by each concept (Figure 3A). Alternatively, we can use the Individuality Space to visualize the individuality of concrete biological entities or types of biological entities (Figure 3B). In each case, the position within

the Individuality Space is approximate and aims to provide a conceptual rather than a quantitative representation.

The Individuality Space works as a general framework for visualizing and exploring the relationship between individuality and selection across different contexts and frameworks. On this, I follow a well-established tradition of depicting degrees of individuality using one- (Pepper and Herron 2008), two- (Birch 2017b, Queller and Strassmann 2009), or three-dimensional (Godfrey-Smith 2009, Salazar and Mitri 2025, Santelices 1999) conceptual spaces constructed from properties or criteria that are thought to be defining or indicative of individuality (e.g., genetic homogeneity, cooperation, bottleneck, etc.).

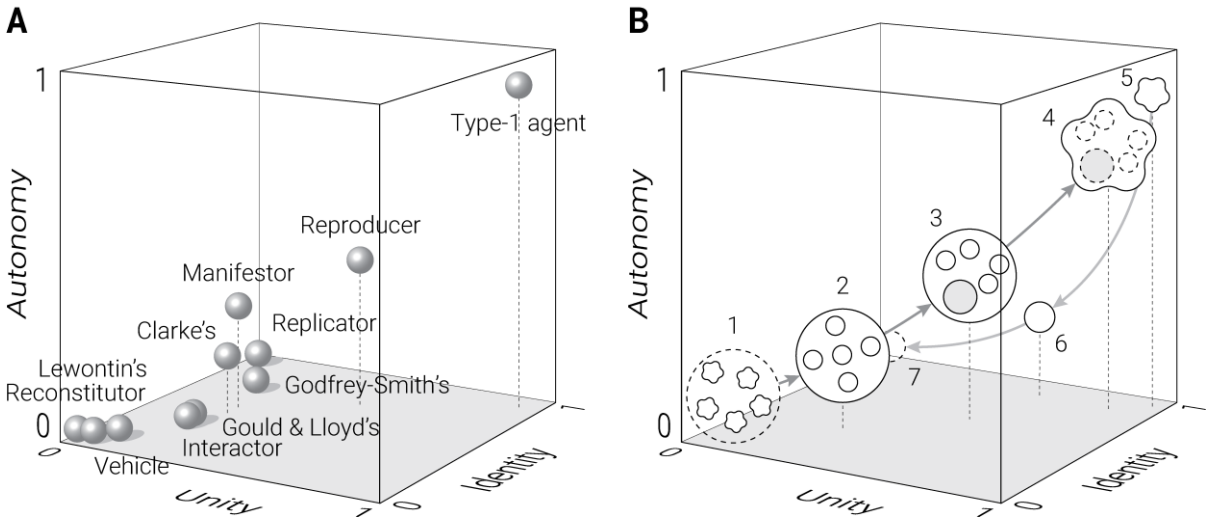


FIGURE 3. INDIVIDUALITY SPACE. The figure represents individuality as a space inspired by Godfrey-Smith's (2009) Darwinian space. The axes correspond to the properties that define individuality: unity, identity, and autonomy. (A) The location of the different types of units of selection is indicated according to the degree of individuality presupposed by each concept. (B) Location of some generalized and idealized types of biological entities: (1) aggregates or loose collectives; (2) collectives without reproduction at their level; (3) collectives with division of reproductive labor among their particles; (4) collective with high degree of functional integration; (5) free-living particles; (6) particles that partake

in collectives; (7) particles that are mere parts of collectives. The arrows indicate the typical pathways of particles and collectives throughout an ETI (see next section and Figure 4 below).

A more recent example of this strategy is a recent paper by Afra Salazar and Sara Mitri (2025). They propose an individuality space with three parameters: "positive interactions," which stands for the degree of cooperation among members of the microbial community; "functional integration," understood as the interdependence that comes with division of labor among the members of the community; and "entrenchment," which stands for the persistence of the community's identity across different environments. Salazar and Mitri then use their framework to compare the position of different types of microbial communities within their space and to propose ways to operationalize each dimension for empirical studies. Interestingly, although a more detailed comparison would be needed, these parameters—tailored to the context of multispecies microbial communities—appear to capture something of the three dimensions of the more general and abstract space I propose here: positive interactions are related to the *unity* of the community, functional integration is linked to its *autonomy*, and entrenchment is associated with its *identity*.

Salazar and Mitri's work thus provides an excellent illustration of how the individuality-space approach could be put to use in concrete biological contexts. Yet, as they note,

> One of the major challenges of our multidimensional space is that it does not tell us how much individuality is enough to exhibit a desired evolutionary response. Nor can we directly map our individuality space to the classic definition of evolutionary individuality of heritable variation. (Salazar and Mitri 2025:7)

The present framework gives a step toward addressing these very challenges by explicitly linking degrees of individuality to the different evolutionary roles that biological entities might

adopt in the process of natural selection. Let us then inspect the Individuality Space as it synthesizes the work carried out in the preceding sections.

THE UNITS OF SELECTION IN INDIVIDUALITY SPACE

Moving from lower to higher degree of individuality, this is, from the lower left corner of the Individuality Space (where the value of each property is 0) toward the upper right corner (where the value is 1), we first notice that individuality is hardly a prerequisite for functioning as a *reconstitutor*, *vehicle*, or Lewontin's *unit of selection*. In each case, the relevant role can be fulfilled by entities that lack unity, autonomy, or identity almost entirely: reconstitutors may be distributed, relational patterns; vehicles may be diffuse and fully dependent on replicators; and Lewontin's units of selection require only minimal conditions of variation, differential fitness, and heritability (Figure 3A). A representative entity in these cases would be a loose collective or a mere aggregate of particles (Figure 3B, 1).

The *interactor* and Gould and Lloyd's *Darwinian individual* also score low: they may lack autonomy and be transient and compositionally unstable entities, although they require enough unity for their constituents to exert mutual influence on fitness. Clarke's *evolutionary individual* likewise requires only minimal individuality for selection to act at its level. However, the individuating mechanisms that define the evolutionary individual are typically evolved features, so I tentatively locate Clarke's evolutionary individual somewhere between the interactor and the *manifestor of adaptation* (Figure 3A). We can think of entities that occupy the region around these units as collectives that do not reproduce at their own level (Figure 3B, 2).

For the most part, the *reproducer* demands a higher degree of individuality, for its requirements of development and material overlap involve the maintenance of some degree of identity over time and at least some autonomy—especially in regards to its reproduction. These, in turn, require a certain degree of unity sufficient to sustain autonomous reproduction (Figure

3A). A reproducer would typically be either a collective with division of reproductive labor among its particles (Figure 3B, 3), or a particle that reproduces with its own machinery (e.g., cells in a multicellular collective). Notice that, in this case, the degree of autonomy of the particle will be lower than the collective that contains it and partially controls its reproduction (Figure 3B, 6).

The *replicator* requires a high degree of identity in the sense of persistence and specificity of structural information, but not unity or autonomy. Close to it I place Godfrey-Smith's *Darwinian individual*, which encompasses entities that are essentially replicators, such as 'scaffolded reproducers' like genes or viruses (Figure 3A). The region of the Individuality Space around the replicator and the (scaffolded) Darwinian individual will customarily be occupied by particles that are totally dependent on the collective for their reproduction and thus are mere parts of it (Figure 3B, 7).

Finally, the *type-1 agent* is the unit that demands the highest degree of individuality: it requires unity and functional alignment of its parts, a high degree of identity that sustains the coordinated activity of the parts, and autonomy that accounts for genuine unity of purpose (Figure 3A). A typical type-1 agent will either be a functionally integrated collective with reproduction at its level (Figure 3B, 4), or a functionally integrated particle that is free-living or a member of a loose group or aggregate (Figure 3B, 5).

Situating the units of selection within the Individuality Space reveals that most of them cluster around low values of each of the three properties (lower left corner of the Individuality Space in Figure 3A), which means that the concepts of units of selection are quite undemanding when it comes to individuality. This implies that *entities with low degrees of individuality can nonetheless play significant evolutionary roles* (e.g., as replicators, reconstitutors, interactors, manifestors of adaptation, etc.). Conversely, this points to the fact that individuality *per se* is rather uninformative about the roles that an entity plays in evolution by natural selection. All

in all, the results of my analysis of the relationship between individuality and the units of selection put pressure on the Individuality Assumption. Being an individual (to a significant degree) is (usually) not a necessary requirement for an entity to be a unit of selection.

Additionally, we see that, of the three individuality-defining properties, autonomy is the least required by the units of selection. The property of autonomy captures the relative independence of an entity from its context, including its constituent particles (in the case of a collective) or the collectives it partakes in (in the case of particles). Thus, the fact that autonomy is largely dispensable suggests the interesting conclusion that the functional roles captured by the different concepts of units of selection are largely insensitive to the distinction between particles and collectives. In other words, the evolutionary roles that each concept of unit of selection encapsulates do not strongly depend on whether the relevant entity is an autonomous whole, a mere part or aggregate, or something in between. This sits well with some central debates in the units-of-selection literature mentioned earlier, such as the problem of cross-level by-products and the problem of pinpointing the level of the manifestor of a given adaptation, where determining the relevant entity to which fitness or adaptive traits should be attributed cannot be decided solely based on the entity's relative autonomy.

Toward an Integrated Approach to Individuality and Selection

With this framework in place, we can now turn to how the notions of units of selection and evolutionary individuality interact, using ETI as a suitable, rich context. The discussion that follows does not intend to do justice to the vast literature on ETI, and a more detailed treatment of this topic is beyond the scope of this review. However, the ideas sketched here will serve as an illustration of how the debates on units of selection and evolutionary individuality could be integrated.

The core problem of ETI research is to explain the evolutionary origins of new levels of individuality that involve the joint reproduction of previously independent reproducers or replicators that come together to form a larger unit. ETI researchers usually consider only one kind of unit of selection: the evolutionary or Darwinian individual.

Now, how could a single type of unit capture the potentially many disparate types of biological entities and evolutionary roles that arise along a transition? Godfrey-Smith (2009) argues that Darwinian individuality comes in degrees, ranging from minimal to marginal to paradigmatic cases. These degrees of Darwinian individuality correspond to the amount of potential to produce evolutionary novelties and complex adaptive traits—that is, *evolvability* (*sensu* Kirschner and Gerhart 1998). Similarly, Clarke (2025) emphasizes that what changes during a transition is the "evolutionary potential"—again, the *evolvability* (*sensu* Brown 2014, Clarke 2025:94)—of the evolutionary individual, which typically increases as the transition progresses. In both views, the *type* of unit of selection remains the same throughout the transition. What varies is its *capacity to evolve* by natural selection—its evolvability—due to the progressive acquisition of mechanisms that allow it to reproduce as a unit (Godfrey-Smith) or concentrate selection at its level (Clarke).

This way of approaching ETI has yielded valuable insights, but also has some limitations. Firstly, as Suárez and Lloyd (2023) have argued, these accounts are rather disconnected from a substantial part of the literature on the units of selection. By considering only a single type of unit of selection and reducing ETI to the change in evolvability, they obscure many other possible questions about the units of selection, especially in the context of ETI research.

Secondly, these accounts are not as straightforwardly connected to individuality as they might seem, for *they understand individuality as evolvability*. In Godfrey-Smith's framework, individuality is largely taken for granted and flattened into a single parameter of "integration"

that constitutes one of the three variables that determine evolvability. In Clarke (especially her most recent work, Clarke 2025), the notion of evolutionary individuality as a scalar property is entirely replaced by the notion of evolutionary potential. Thus, although Godfrey-Smith's unit in ETI is called Darwinian *individual* and Clarke's is called evolutionary *individual*, individuality *per se* does not appear to do much work in these approaches. Rather, the substantive explanatory work is carried by the idea of relative capacity to evolve by natural selection. In this sense, Godfrey-Smith's and Clarke's "individuals" might more neutrally and accurately be labeled simply as *units*.

In any case, I need not take stance here on whether this way of framing ETI is the correct one or whether we should favor a disambiguating, units-of-selection approach instead. Rather, I submit that my approach facilitates the integration of the units-of-selection perspective with the evolutionary individuality approach to ETI and, in turn, connects both more tightly to the notion of individuality.

INDIVIDUALITY AND SELECTION IN FLUX

In the previous section, I showed how different types of entities occupy different regions of the Individuality Space (Figure 3B). We can now go one step further and interpret their positions not as fixed points but as potential stages along trajectories of increasing or decreasing individuality during ETI (see arrow paths in Figure 3B). This idea is not new. Godfrey-Smith (2009:103), for example, conceptualizes ETI as movements of Darwinian populations through the Darwinian space, where collectives shift from marginal to paradigmatic forms of Darwinian individuality, while their constituent particles move in the opposite direction across the same space as they become progressively "de-Darwinized." Heikki Helanterä and Tobias Uller (2019) further explore and visualize this idea in the context of eusocial insect colonies. Similarly, Salazar and Mitri (2025) propose that multispecies

microbial communities can be thought of as traversing an individuality space as they undergo ETI.

Interpreted this way, the Individuality Space shows how much individuality the entities have at each point along an ETI. Moreover, by comparing Figures 3A and B, I concluded in the previous section that entities with relatively low degrees of individuality—e.g., collectives at early stages of a transition—can nevertheless play significant evolutionary roles. In other words, the degree of individuality characteristic of the regions the entities traverse during transitions is sufficient for those entities to acquire a variety of evolutionary functions and thus become different types of units of selection (Figure 3A).

These observations can be made more precise by considering how the redistribution of evolutionary roles occurs during an ETI. According to Suárez and Lloyd's (2023) interpretation, an ETI typically starts with a group of lower-level particles that are simultaneously reproducers, interactors, and manifestors/type-1 agents, and a higher-level collective that is an interactor but not a reproducer or unit of adaptation. The transition involves the gradual transmission of the reproductive capacity and export of fitness from the particles to the collective by the accumulation of adaptations related to reproduction at the collective level driven by natural selection acting at that level. The accumulated adaptations include policing mechanisms (*sensu* Clarke) that contribute to the progressive de-Darwinization of the particles (*sensu* Godfrey-Smith) and their integration into the increasingly individualized collective. The result of the transition is a higher-level entity that is simultaneously an interactor, reproducer, and unit of adaptation, and which can continue evolving as an interactor and accumulating further adaptations at its level. Meanwhile, the lower-level particles might retain some of their original roles (e.g., reproducer).

We can zoom in on an idealized and simplified ETI to see how this works in a bit more detail. For this purpose, I will assume a "fraternal" transition, in which entities of the same kind

come together to form a group (in contrast to an "egalitarian" transition, which involves the association of entities of different kinds; Queller 1997). Also, I will assume that the transition leads to a new higher-level entity, although transitions might occur in the opposite direction as well (e.g., see Danforth 2002, Herron and Michod 2008). Finally, I will recognize five, rather than the usual three, phases in the transition (e.g., Bourke 2011, Rose and Hammerschmidt 2021, West et al. 2015), which will give us a finer-grained view of the different roles that the entities can play throughout the transition. The description of this hypothetical ETI follows closely the diagram in Figure 4, so readers are encouraged to keep it in view.

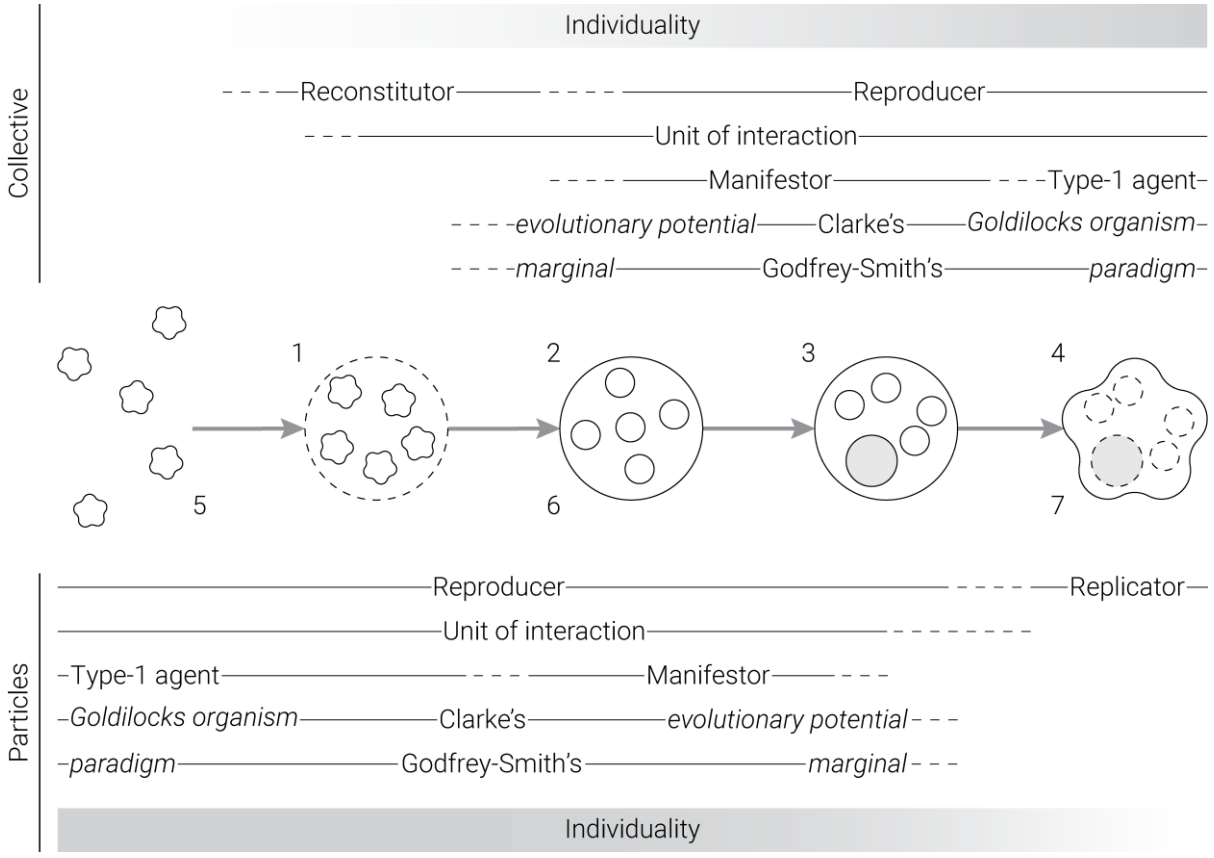


FIGURE 4. UNITS OF SELECTION AND THE EVOLUTIONARY TRANSITIONS IN INDIVIDUALITY. The diagram shows a simplified and idealized evolutionary transition in individuality and the different evolutionary roles in relation to natural selection that the collective (above) and the particles (below) might adopt

throughout the transition. The numbers link the entities depicted here to the same entities in Figure 3B above.

We start with a population of independent, free-living entities at the lower level (Figure 4, left). These fulfil the three main evolutionary roles: they are at once units of interaction, heredity, and adaptation. In particular, since they are not part of a structured group, they are the exclusive level of selection (they are "Goldilocks organisms" and "paradigm" Darwinian individuals in Clarke's and Godfrey-Smith's terms, respectively). Their degree of individuality is close to 1 for each of the individuality-defining properties (unity, identity, and autonomy). In a second stage, certain structural patterns might start to become reconstructed in each generation, despite the fact that the entities do not form proper groups and do not reproduce as a whole. In other words, a reconstitutor emerges at the collective level with a very low degree of individuality of its own.

The next stage might come shortly after. The interacting entities become particles of a poorly-individualized group defined by fitness-affecting interactions. The particles still reproduce on their own and there is no reproduction at the collective level. However, selection now acts *also* at the collective level, which then becomes an interactor. From then on, it becomes a (marginal) Darwinian individual and its evolvability *qua* evolutionary individual starts to build up. At this point, determining the level at which selection becomes a non-trivial task (recall the problem of cross-level by-products).

Selection at the collective level starts accumulating adaptations—first product-of-selection adaptations, then incipient engineering adaptations. Thus, the collective becomes a manifestor of adaptation, and determining the level at which the manifestation of adaptations occurs becomes an issue. Also, around the fourth stage in our hypothetical ETI, the accumulation of adaptations related to reproduction at the collective level (e.g., the division of reproductive labor among the particles) transforms the collective into a reproducing entity. For the particles,

this means that most of them become dependent on the collective, the evolved policing mechanisms increasingly de-Darwinize them, and their evolvability drops. The individuality of the collective rises, and that of the particles decreases because they relinquish part of their autonomy to the collective.

The transition ends with the collective becoming a functionally integrated, highly individualized entity. It approaches the Goldilocks or paradigm state, and its evolvability is high, which translates into further accumulation of engineering adaptations. The particles might continue to function as (weak) interactors and reproducers at their level (e.g., the somatic cells in a multicellular organism), but some of them might eventually become replicators.

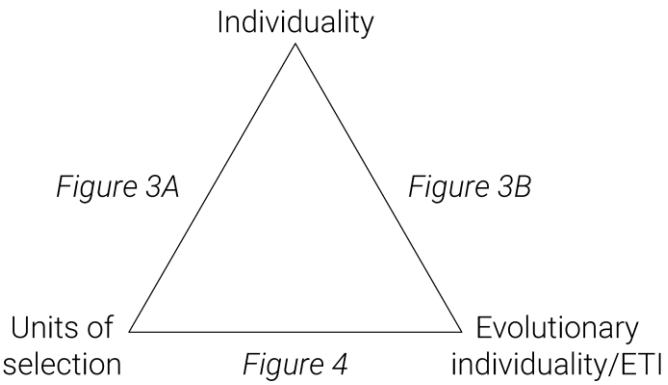
Of course, real ETI may have different starting and end points and follow different trajectories, and the sequence of events and evolutionary roles need not occur exactly as I described it in this idealized scenario. Still, this example, combined with Figure 3, suffices to illustrate how the evolutionary roles defined by the units-of-selection approach, the evolvability captured by the evolutionary individuality/ETI approach, and individuality are related.

CONCLUSIONS

In this review, I have undertaken a systematic exploration of the relationship between individuality and natural selection. In particular, (i) I have assessed whether the Individuality Assumption is warranted through a detailed analysis of each of the main kinds of units of selection and evolutionary individuals that have been proposed. (ii) I have provided further clarification of the relationship between the concepts and literatures of units of selection and evolutionary individuals. Finally, (iii) I have linked the notions of units of selection and evolutionary individuality with the more fundamental idea of individuality that subtends these

1228 debates, paying special attention to how these three conceptual knots are interwoven across
1229 ETI.

1230 These tasks (i–iii) come together in an integrative framework that relates the units of
1231 selection to evolutionary individuality/ETI and, in turn, relates these to individuality (Figure
1232 5). To explore this framework, I have proposed an Individuality Space that represents the
1233 relationship between individuality and selection both synchronically (Figure 3) and
1234 diachronically during ETI (Figure 4).



1235

1236 FIGURE 5. INDIVIDUALITY AND SELECTION REDUX. The diagram represents the synthetic framework I
1237 propose in this review, namely, a triangulation between the units-of-selection approach, the evolutionary
1238 individuality-ETI framework, and individuality in a general, abstract sense. The links connecting each
1239 of these three facets are summarized in the referenced figures.

1240 I would like to conclude this review with a brief recapitulation of its central take-home
1241 messages:

1242 1. A given kind of biological entity (e.g., a gene or an organism) can occupy different
1243 functional roles in evolution by natural selection (e.g., replicator, reconstitutor,
1244 interactor, manifestor of adaptation). Conversely, the same role can be realized by

different kinds of entities, including some that are not standardly regarded as individuals or are only marginally so (e.g., genes, ecological assemblages, species).

2. The notions of units of selection and evolutionary individuals do not require much individuality, which implies that entities with low degrees of individuality can play significant evolutionary roles. Thus, individuality *per se* is rather uninformative about the roles that an entity plays in evolution by natural selection.
3. Among the three dimensions of individuality—unity, identity, and autonomy—autonomy is least required for an entity to count as a unit of selection or evolutionary individual. Evolutionary roles are thus largely insensitive to whether an entity is an autonomous whole, a mere part or aggregate, or something in between, and therefore to the distinction between particles and collectives.
4. Taken together, conclusions 1–3 undermine the Individuality Assumption, according to which an entity must be an individual to serve as a unit of selection. Being an individual (to a significant degree) is generally not a necessary condition for being a unit of selection, and therefore the relationship between individuality and selection should be explicitly theorized rather than being taken for granted.
5. Current notions of evolutionary individuality appeal to individuality largely in name only, as they primarily track an entity's *evolvability* rather than its *individuality*. Theoretical work should clarify how, and to what extent, individuality is related to being an evolutionary or Darwinian individual.
6. More generally, talk of "individuals" should do substantive conceptual work and be grounded in an explicit philosophical account of individuality. Where no such account is provided, the language of individuality adds little beyond rebranding, and more neutral terms such as "unit" should be preferred.

7. Individuality can be broken down into three components: unity, identity, and autonomy. Since these are scalar properties, they can be represented as the dimensions of a three-dimensional Individuality Space. This heuristic tool provides a richer view of how individuality varies in different cases and may facilitate conceptual standardization and empirical operationalization.
8. Research on individuality and selection should attend more closely to the distinct evolutionary roles entities play (e.g., reproducer, interactor, manifestor of adaptation) and to how these roles relate to different dimensions of individuality, rather than treating such cases as merely "incomplete" or "marginal" vis-à-vis a "paradigmatic" state.
9. Similarly, ETI research would benefit from a multidimensional, stepwise analysis of how evolutionary roles are gradually acquired or redistributed, rather than construing transitions solely in terms of degrees of evolvability. This perspective would accommodate the evolutionary roles of contemporary collective forms (e.g., symbioses, colonies, and microbial consortia) and may shed light on ETI mechanisms and pathways.

Glossary

Darwinian population,

Marginal: A population of entities that meets the conditions for evolution by natural selection only partially or weakly, so its evolvability is low.

Paradigm: A population of entities that (almost) fully satisfies the conditions for evolution by natural selection and thus possesses the potential to produce evolutionary novelties and complex adaptive traits (i.e., high evolvability).

Evolutionary potential: A scalar property that measures the extent to which selection is concentrated on a given level by the suppression of selection at lower levels due to the action of individuating mechanisms, and which increases through a typical **Evolutionary transition in individuality (ETI)**. *Syn. Evolvability*.

Evolutionary transition in individuality (ETI): A process of emergence of a reproducing entity at a new **Level of individuality** by the association of lower-level entities that previously had the capacity to replicate or reproduce independently (or the reverse of that process).

Goldilocks organism: a. An **Evolutionary individual-b** with high **Evolutionary potential**. *Syn.* **Paradigmatic individual-a** *or* **b**. **b.** An **Evolutionary individual-b** with maximum **Evolutionary potential** that represents the idealized end result of a typical **Evolutionary transition in individuality (ETI)**. *Syn.* **Paradigmatic individual-c** *and* **-d**.

individual,

Biological: A relatively well-delineated entity that participates in evolutionary, physiological, or other biological processes. *Sometimes used as a synonym of* **Evolutionary individual**, **Physiological individual**, **Organism**.

Darwinian: a. A member of a **Darwinian population** (Godfrey-Smith). **b.** A **Unit of interaction**. *Syn.* **Interactor** (Gould and Lloyd). *Sometimes used as a synonym of* **Evolutionary individual**, **Unit of selection**.

Evolutionary: a. An entity that evolves, has evolved, or has the capacity to evolve by natural selection. **b.** A living entity or group of living entities that have individuating mechanisms that allow them to form populations that can evolve by natural selection (Clarke). **c.** A genetically homogeneous entity or lineage of entities that develops from a fertilized ovum. *Syn. Genetic individual* (Janzen). *Sometimes used as a synonym of* **Darwinian individual**, **Organism**, **Unit of selection**.

Metaphysical: An entity defined by the scalar properties of unity, identity, and autonomy. *Unity* denotes the cohesion and boundaries that integrate the entity's parts into a coherent whole. *Identity* refers to the entity's distinctness and persistence. *Autonomy* captures the capacity of the entity to exist and persist independently, rather than as a mere part or aggregate of other entities.

Paradigmatic: (Let *X* be a **Biological**, **Darwinian**, **Evolutionary**, or **Physiological individual**) **a.** A clear-cut, unproblematic example of *X*. **b.** A highly individualized *X*. **c.** A benchmark against which the

individuality of *X* is contrasted. **d.** A limit that *X* approaches in development or evolution. *Sometimes used as a synonym of* **Organism**.

Physiological: A functionally integrated whole made of parts held together by metabolic, immunological, or other types of interactions. *Sometimes used as a synonym of* **Biological individual**, **Organism**.

Individuality Assumption: A claim popularized by David Hull, according to which being an individual (roughly characterized as a **Metaphysical individual**) is a necessary condition for an entity to qualify as a **Unit of selection**.

Interactor: A **Unit of interaction** that interacts as a whole with the environment in a way that replication or reproduction is differential. *Sometimes used as a synonym of* **Darwinian individual-b**, **Vehicle**.

Level

of individuality: A set of **Biological**, **Darwinian**, **Evolutionary**, or **Physiological individuals** of the same kind within a biological hierarchy. If the individuals are evolutionary or Darwinian, the level of individuality is also a **Level of selection**.

of selection: A set of **Units of selection** or **Evolutionary** or **Darwinian individuals** of the same kind that interact in a way that mutually affects their fitness.

Manifestor of adaptation: A **Unit of adaptation** that bears trans-temporally accumulated engineering adaptations due to past selection.

Organism: A self-organizing, self-maintaining, autonomous living system made of functionally integrated parts. *Sometimes used as a synonym of* **Biological individual**, **Evolutionary individual**, **Paradigmatic individual**, **Physiological individual**, **Unit of adaptation**.

Reconstitutor: A **Unit of heredity** consisting of a structure that is recreated in each generation without replication or material overlap.

Replicator: A **Unit of heredity** whose structure is differentially copied.

Reproducer: a. A **Unit of heredity** that transmits, through material overlap, the capacity to develop the capacity to reproduce (Griesemer). **b.** An entity that forms parent-offspring lineages. *Scaffolded* reproducers are entities that do not reproduce by themselves but are reproduced by other entities or as the result of the

reproduction of a larger entity they partake in. *Simple* reproducers can reproduce independently. *Collective* reproducers reproduce as a whole and their parts also have the capacity to reproduce (Godfrey-Smith).

Type-1 agent: A **Unit of adaptation** whose adaptive traits contribute to a single overall goal ("unity of purpose"). *Sometimes used as a synonym of* **Organism**.

Unit

of adaptation: An entity that shows adaptive traits evolved by natural selection.

of heredity: An entity that transmits phenotypic variation across generations. *Syn. Unit of reproduction*, *Reproductive unit*.

of interaction: An entity that shows phenotypic variation and differential fitness. *Syn. Target of selection.*

of selection: a. An entity that participates in the process of natural selection as a **Unit of adaptation**, **heredity**, or **interaction**, or as a **Darwinian** or **Evolutionary individual** (Suárez and Lloyd). **b.** An entity that has heritable variation in fitness (Lewontin). *Syn. Unit of evolution*, *Evolutionary unit*. *Sometimes used as a synonym of* **Darwinian individual**, **Evolutionary individual**, **Interactor**.

Vehicle: A **Unit of interaction** that contains and is the phenotypic expression of **Replicators**.

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