Individuation, Process, and Scientific Practices

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Individuation of Developmental Systems

A REPRODUCER PERSPECTIVE

James Griesemer

7.1 Process-Relativity of Individuality Concepts

In my view, the concept of "individuality," especially as it is used in the sciences, is a scientific-theoretical concept rather than a logical or metaphysical concept to which scientific usage is somehow obliged to conform. While philosophers have had much to say about individuality (e.g., Goodman and Leonard 1940; Strawson 1959; Wiggins 1980), I think we learn more about the concepts, claims, and consequences of individuality in the sciences by supposing it is a theoretical term that can mean different, even conflicting, things in different theoretical contexts, such as in different scientific specialties and disciplines with different research questions, projects, and phenomena to consider, rather than a logical or metaphysical term that should have a single, best, all-purpose fixed meaning. In this chapter, I limit my argument to concepts of biological individuality, focusing on concepts used in some parts of evolutionary biology. Aspects of what I shall argue may generalize. It is beyond my scope to speculate about other sciences.

There is great variety in usage of the term "individual" among biological specialties, from a ramet, genet, or a module in botany; to a zooid, person, or sorus in zoology; to a cell in microbiology; to a behaving subject in ethology; to an organism, species, or unit of selection in evolutionary biology. Most biologists use the term "individual" interchangeably with "organism" except when they are discussing questions of units and levels of evolution, though the problem of individuality as philosophers understand it is then merely transferred to the question of what is an organism.

My thesis is that, despite all the variety of usage, concepts of biological individuality suitable for evolutionary biology involve two senses of *process-relativity*. The concept depends on (1) some *empirical process* we take to be operating in the world that we humans talk about, try to understand, predict, explain, or control; and (2) a *tracking process* that we humans perform, through which we attempt to do the things described in (1). In other words, concepts of individuality depend on the empirical process of concern to the humans who investigate, use, or otherwise rely on it to understand and interpret biological entities and phenomena and also on what tracking processes they perform to investigate them with. Individuality concepts thus have a dual character: they are partly about processes in the world beyond and around us and partly about us, in so far as our concepts are linked to the mode and manner of our tracking engagements with the world.

We need concepts of *individuality* in science as well as in other practices of everyday life in order to tell stories about what goes on in the world, do science, and make attributions of properties, relations, responsibility (causal or moral), and standing (e.g., epistemic, moral, legal). We also need concepts (plural) of *individuation* in order to count, distinguish, and relate what we find when we engage the empirical world of processes. Differently put, we need to individuate—distinguish one individual from another—in our varied tracking practices to track the varied processes we discover and order them into countable and accountable "things": lineages, groups, kinds, and so forth. Scientists have need of, as nominalists like Nelson Goodman might say, a logic of individuals whatever their metaphysical commitments or lack thereof.

My goals for the chapter are to (1) illustrate process-relativity of biological individuality by discussing just two different kinds of attempts to articulate concepts of evolutionary individuality, one based in natural selection theory, the other based in a theory of biological reproduction; and (2) display how the tracking activities of scientific practices are entwined with the empirical processes on which both individuation and individuality depend. I will not attempt to survey the vast and growing literature on individuality in biology (e.g., see Clarke 2010; Bouchard and Huneman 2013; Guay and Pradeu 2016). In the final section, I will make some remarks intended to motivate a search for extrapolations and applications beyond the narrow scope I have set for my discussion.

7.2 Individuality, Individuation, and the Practice of Evolutionary Theory

Much of the discussion of biological individuality in philosophy of biology has been driven by the units of selection problem. To what "units" does Darwin's theory of evolution by natural selection apply? Is there one (kind of) unit of selection or many? Organisms? Groups? Species? Genes? What evolutionary "interests" lead potentially self-interested entities to function as parts serving the collective interest of a whole, possibly even in conflict with their own self-interest? Can Darwin's theory of the evolution of populations and species by means of natural selection among organisms be generalized by abstracting from a characterization of individual *as organism* (Griesemer 2005), across the compositional hierarchy from molecules to man or from genes to species (Lewontin 1970), or perhaps across a functional hierarchy of replicators and interactors (Dawkins 1976; Hull 1988)? Differently put: Is "organism" just one form or manifestation of biological individuality among many? What is an organism anyway? Are colonial animals individual organisms? Are modular plants lacking (early) germline segregation individual organisms (Jackson, Buss, and Cook 1985; Buss 1987)?

I need not rehearse the history of this problem. It is sufficiently well-known to be reviewed in encyclopedia articles (Lloyd 2012). My problem starts, instead, with two prior questions. Is the generalization of Darwin's theory the right starting point for inquiring into the nature and characterization of evolutionary individuality, even for the sake of answering questions about the units of selection? Many philosophers of biology assume so, or at least became aware of the problem through pondering the nature and structure of evolutionary theory (e.g., Sober 1984; Sober and Wilson 1998; Godfrey-Smith 2009). Many began thinking about the problem at a time (1960s–1980s) when the status of biology and theories in biology were in question by philosophers of science of an earlier era, trained to valorize physics as exemplary of science in general, who judged biology to be lacking important qualities of "mature" sciences. At stake was not only how to understand units of selection, but whether Darwin's Principles filled the role of laws of nature in a (neo-)Darwinian theory.

On the other hand, many biologists discovered the problem of units of selection because they were dealing with empirical phenomena that seemed puzzling against the backdrop of the old catechism that genes are the units of heredity, organisms are the units of selection, and populations are the units of evolution (e.g., Wade 1976, 1977, 2016). Many plants, animals, fungi, and bacteria have complex life cycles or colonial social organization, suggesting that looser organization than that of vertebrate animals is sufficient for individuality. A fair few of these behave in ways strikingly contrary to familiar individual human behavior; for example, the cellular slime molds whose physically attached "parts" disaggregate and aggregate (Bonner 1967). Organisms may have tissues that are not at all germ-like yet which can initiate new reproductive lineages (buds, branches, cuttings). Groups of organisms may themselves reproduce, develop, behave, or evolve in organism-like ways (eusocial colonial animals).

Groups of organisms can be made to respond *as groups* to selection in the laboratory (e.g., flour beetles; see Wade 1976). Their evolutionary responsiveness seems to suggest selection may operate at more "levels" than only that of self-interested organisms competing for resources or mates (e.g., house mice carrying t-alleles in some gametes and some groups but not others; Lewontin 1970; discussed in Wimsatt 1980; Lloyd 1988). Not to mention that there are entities which seem to evolve, yet are distinctly un–organism-like, such as retroviruses and maybe prions and some transposons (see Godfrey-Smith 2009) as well as symbiotic associations of organisms, such as the Hawaiian bobtail squid and its light-emitting bacterial symbiont, *Vibrio* (McFall-Ngai et al. 2013).

In those early decades of the units of selection problem, only a few philosophers, in collaboration with scientists, approached the problem of units of selection from the perspective of *experimental* rather than theoretical investigation of group phenomena (e.g., Antonovics et al. 1988; Griesemer and Wade 1988). In experiments, the problem of *individuation* raises immediate and practical concerns for experimental design, management, and data collection, whatever one's theoretical or metaphysical attitude toward concepts of *individuality*. Empirical entities such as vials of flies or beetles, Petri dishes of bacteria, or hives of bees must be labeled and tracked, regardless of whether they are treated as groups or individuals. I suggest the question of biological individuation is practically, empirically, logically *prior* to the theoretical units of selection individuality question, even if the "ultimate" process of evolution is historically prior to the "proximate" processes structuring individuality. Empirical interest in some particular (or particular kind of) biological "system" whose physiology, ecology, development, reproduction, life cycle, or behavior has some organism-like and some group-like (or at least non–organism-like) aspects or activities demands attention be paid to the tracking problem—that is, the problem of individuation—regardless of theoretical commitments. Moreover, theory must eventually face the practical, empirical, and logical problems with regard to the problem of adducing evidence anyway.

Mayr's (1961) labeling of biological problems and processes as proximate or ultimate and Dobzhansky's declaration (1973) that nothing in biology makes sense except in the light of evolution notwithstanding, it is equally clear that evolution does not make sense except in the light of the rest of biology (Griesemer 1994). So, it is a toss-up which *concepts* must "come first" in order to understand "the rest," never mind which *processes* must have come first in order to *evolve* the rest. After all, those biologists who arrive at the units of selection question starting with puzzles about the nature and scope of Darwinian theory must have in mind some biological "content," some empirical phenomena, through which heritable variation in fitness can be generated, else the theory is merely an empty formalism. What salience do these biologically, epistemically, logically prior concerns have for the problem of evolutionary individuality? And, if the prior concerns grow out of empirical practices of inquiry into the behavior of biological systems, what relevance does that grounding in non- or pre-evolutionary practice, rather than in evolutionary theory, have for understanding biological individuality? What salience, for example, does the fact that John Tyler Bonner (1952, 1967) sought to understand slime mold *morphogenesis* and to use it as a model system for understanding *developmental regulation* have for the role his "system" now plays in arguments about the *evolution* of individuality (Buss 1987; Godfrey-Smith 2009; Queller and Strathmann 2009)?

My own philosophical interest in biological individuality grew out of the units of selection problem—I was taught by Bill Wimsatt while units of selection was *the* problem in philosophy of biology; I was also taught by biologists who came to the problem through experimental and field studies of evolution (Michael Wade, Stevan Arnold), as well as by theoreticians (Russ Lande). I have become convinced that units problems in evolutionary biology must be addressed first and foremost, *prior* to questions about natural selection, drift, and other "forces" of evolution, in terms of developmental, reproductive, and ecological processes. And I have become convinced that the way to interpret how biologists understand developmental and reproductive processes is to study how they individuate processes in biological practice; that is, how they track reproduction and development empirically (Griesemer 2007), as parts, Ken Waters would say, of their "investigative strategies" (Waters 2008). Even if the "individuality" problem is logically (or metaphysically) prior to the "individuation" problem, individuation in practice is practically prior to the "individuality" problem in the sense that we can discover new ways to think about individuality through practical commitments to individuate in particular ways, respects, and degrees, but the reverse is an armchair problem for metaphysicians alone.

One way to grasp the priority of the problem of individuating reproduction processes to a problem of biological individuality founded on Darwin's principles is to consider the place of Malthus's "principle of population" in relation to Darwin's principles. Recall Malthus's principle: population, unfettered, tends to grow geometrically while food supply tends to grow, at best, arithmetically, so population will inevitably exceed food supply and individuals will suffer unless population is regulated (Malthus 1826). It remained unclear, after Lewontin's (1970) work to regiment and generalize Darwin's principles, whether or not Malthus's principle should be considered prior to (as presupposition or axiom), as one of, or rolled into (as conceptually embedded in) Darwin's three principles of variation, fitness difference, and heritability. Lewontin (1970) presented Malthus's principle as a presupposition of Darwin's principles. Maynard Smith (1987) made the connection between Malthus and Darwin in terms of a principle of "multiplication," which he included *within* his formulation of "Darwin's Principles"—multiplication, variation, and heritability—demoting fitness differences to an add-on in the special cases where evolution occurs *by means of* natural selection, rather than, say, by means of drift alone. Most formalizers after Lewontin seem to embed Malthus's principle within Darwin's rather than stating it as a separate principle or presupposition, but are never entirely clear how the embedding works. I favor the clarity of Maynard Smith's approach, but Maynard Smith didn't go very far toward characterizing his principle of multiplication, nor in distinguishing a *biological* concept of multiplication (i.e., reproduction) from other, nonbiological processes of duplication, multiplication, or copying (see Griesemer 2000*a*, 2000*c*, 2005). My view is that the units of selection question must begin with an answer to the question of what sorts of "things" can *potentially* be units of selection, and only then can we move on to the question under what circumstances and conditions does one of these potential units *actually* become a unit with an "opportunity for selection" (Moorad and Wade 2013). Therein lies the question of how and when something *becomes* an evolutionary individual. Emphasis on becoming shifts the problem to individuation of processes from individuality of things.

One kind of answer to what can potentially be a unit of selection, and therefore an evolutionary individual, is "biological individuals." Richard Lewontin (1970) and David Hull (e.g., 1980, 1988) explored this kind of answer in depth. Lewontin appealed to traditional notions of entities that reside at "levels" of organization other than that of organisms—genes, cells, groups—to get his abstract notion of individuality going. Hull (and Dawkins 1976, 1982) appealed to functions of replication and interaction, though these concepts depended on received views of DNA replication and molecular, cellular, and organism interaction, together with a metaphysical interpretation of Kripke's theory of proper names as rigid designators (see Hull 1980, 1981) to get his notion of individuality going.[1]

Both of these approaches to what can be a unit of selection have been challenged. My own challenge was based on the argument that each ends up question-begging because they have to assume that these highly evolved entities at levels of composition or function can nevertheless exist prior to the evolution of genes and cells (Griesemer 2000*a*, 2000*b*, 2000*c*, 2005). I think these approaches carry a germ of truth, but it is tricky to avoid the question-begging circularity of appeal to already evolved entities to characterize evolutionary individuality. Theories of evolutionary transition (Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999) put pressure on these philosophical approaches to units of selection by recognizing that the compositional levels of evolution and the functioning of entities at those levels *themselves* evolved. Dawkins (1976, 1982), and many origins of life researchers who favor a "replicator first" approach (see Griesemer 2008), attempt to cut this Gordian knot by proposing that life began with a spontaneously formed entity which was at once a first replicator and an interactor.[2] As is well-known to philosophers, "unmoved mover" arguments are mainly trained on metaphysical rather than scientific problems.

More recently, some authors have widened these approaches to regard biological or evolutionary "individuality" as a degree property (e.g., Queller and Strathmann 2009; Godfrey-Smith 2009, 2013). Queller and Strathmann (2009: 3143), for example, take a hallmark of organismality to be "high cooperation among the parts . . . nearly free of conflicts." We might generalize that idea directly from "organismality" to "biological individuality." Their paper implies that many traits usually associated with biological individuality ("physical contiguity,

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[1] For a disentangling of Hull and Dawkins, see Griesemer (2005).

[2] "Spontaneous" here means "by chemistry alone," but as this is often characterized as historically prior to the origin of systems capable of evolution, it also becomes question-begging to appeal to chemistry as prior to biology in these evolutionary terms. This form of "tautology problem" can be stated thus: "What is alive? Those chemical systems which can evolve by means of natural selection. What can evolve by means of natural selection? Those chemical systems which are alive."

indivisibility, clonality or high relatedness, development from a single cell, short-term and long-term genetic cotransmission, germ–soma separation and membership in the same species") really are "non-essential." Queller and Strathmann (2009: 3143) suggest treating organismality as a degree property relating degree of cooperation to degree of conflict among parts implies that "we accept some unconventional organisms, including some social insect colonies, some microbial groups and viruses, a few sexual partnerships and a number of mutualistic associations" (2009: 3143).

While this degree-property characterization of biological individuality opens a path to the *evolution* of multiple levels of evolutionary units (evolutionary transition) or evolution of novel functional properties of replicators and interactors (evolution of genetic coding, evolution of genotype/phenotype distinction) by adaptive changes in degree, it still does not address what kinds of entities are candidates—have the potential—to evolve these properties of individuality from a low to a high degree and thus what biological individuality means. Moreover, it does not distinguish a scientific-theoretical view of "part-hood" as involving something like "processes that hang together which interested scientists may track" from a metaphysically permissive view admitting as individuals whatever collections of entities satisfy a logic of mereology. When is an entity a part, and when is it not? The answer cannot be that an entity is a part so long as it, along with other parts, "shows a high degree of cooperation and is nearly free of conflict with the others" on pain of the same kind of circularity (part-hood delimited by individuality; individuality delimited by part-hood) that threatens earlier views on biological individuality.

So long as the characterization, criterion, or definition is "instrumental" or "pragmatic"—part of an empirical tracking practice rather than embedded in a theoretical concept of a formalized theory of evolution—I think such circularity is relatively harmless because *pragmatically* the limits of investigator interest or ability to measure empirical quantities of interest—such as fitness, cooperation, or conflict—halts circular reasoning with a generic, doubt-stopping solution: "it's what we could afford to do, so that's the best we can do under the circumstances of our investigation."

A different kind of answer to the question of what can *potentially* be a unit of selection, looks to the processes (rather than properties or qualities) which must operate for there to be biological individuals of the above kinds in the first place, let alone individuals subject to natural selection. Must there already be, in other words, some sort of biological individual to be a candidate Darwinian (or evolutionary) individual? And what sort of biological properties underpin biological individuality, if not status as replicators or interactors or cooperators? What processes are necessary for replication, interaction, cooperation, or selection to operate but which do not thereby constitute replication, interaction, cooperation, or selection processes (i.e., which are not in themselves instances of those processes)?

This second, “prior process” kind of approach takes biological individuality to be a problem prior to questions of units of selection and evolutionary individuality, though, in a way, so did the direct approach through appeal to biological individuals since they ended up appealing to some more fundamental property of replication, interaction, cooperation, or selection to interpret concepts of part, organism, and biological individuality.[3] But those previous “direct” approaches all embedded the individuality concept in solutions to the units of selection question, which is to court circularity if those properties (replication, interaction, cooperation) are themselves to be understood as *outcomes* of selection processes. If to be a biological individual is to be (potentially) a unit of selection, then appeal to biological individuality cannot answer our questions about what can be a unit of selection.

My own prior process approach is to take reproduction to be a process conceptually prior to selection/evolution and to take “reproducers” as units which can potentially be units of evolution and selection (Griesemer 2000*a*, 2000*b*, 2000*c*, 2002, 2006*a*, 2014*a*, 2014*b*, 2016). I characterize reproduction in a way that does not depend on properties which themselves require evolutionary explanation. In pursuing that approach, the abstract conceptual considerations are paired with practical, empirical considerations. To *characterize* a biological process of reproduction is also to characterize (or presuppose or imply) practices for empirically tracking reproduction, development, and heredity. For evolutionary purposes (typically) a reproducer approach *foregrounds* hereditary rather than developmental aspects (see Griesemer 2007). That foregrounding, however, is an artifact, I believe, of the way the history of the units of selection and Darwin’s Principles problems unfolded. The foreground–background balance between heredity and development is shifting with the rise of evo-devo (e.g., Wagner 2014), eco-devo (e.g., Gilbert and Epel 2009; Sultan 2015), and calls for extended or alternative synthesis to the “modern synthesis” of genetics, systematics, and evolution (e.g., Pigliucci and Müller 2010). In my view, formal characterization in a theory, or “formalization,” of a concept specifies not only its meaning in a web of theoretical meanings, but also its empirical role in process tracking because, to have empirical content, the theory must also specify a domain over which the theory delimits and guides empirical inquiry. Formalization includes this latter empirical guidance aspect and not only production of a theoretical “formula” (Griesemer 2013).

In the remaining sections, I consider two kinds of approaches to the question of evolutionary individuality which consider prior processes and empirical tracking together. In Section 7.3, I consider an approach which seems to me to

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[3] Examples of prior process approaches include focus on properties like autonomy (e.g., Ruiz-Mirazo and Moreno 2012; Moreno and Mossio 2015), autopoiesis (Maturana and Varela 1980), and self-organization (e.g., Kauffman 1993). A synthetic approach combining many of these can be found in Gánti (e.g., 2003). A critique of these many diverse kinds of definitions of individuality can be found in Clarke (2010).

avoid circularity despite appealing to evolutionary concepts in order to articulate definitions of individuality. It avoids circularity by focusing on the *practice* of evolutionary theorizing and evaluating evidence rather than on designing concepts and principles of a generalized evolutionary theory per se. Charles Goodnight (2013) considers the practice of *assigning* fitness and considers, as one of three definitions, *that to which fitness is assigned in an evolutionary explanation* as a concept of evolutionary individuality. While depending heavily on concepts central to Darwinian and neo-Darwinian theory, Goodnight's approach does not define "individual" in terms of fitness (or selection), but rather appeals to certain kinds of practices (fitness *assignment*) which are necessary to *individuate* entities subject to evolutionary explanation (i.e., necessary to detect and track things that *have* [their own] fitness values). Before turning to Goodnight's approach, I need to consider tracking practices more generally.

A hallmark of tracking is the practice of introducing a "mark" into a process by causally intersecting with it and collecting traces from the marking interaction for use in representations of the process as a sequence of traces. That's a complicated, fancy way of saying that if you want to track something, you either have to keep your eyes on it, mentally noting its location continuously, or mark it in some way so that you can track the marks, noting its location episodically by collecting the traces the mark leaves (Griesemer 2007). I track my carry-on bag through airport screening by watching it go down the conveyor belt, into the scanner, out of the scanner, and down the belt on the far side. I cannot track a package in a similar way after I turn it over to FedEx, nor can any single FedEx employee, so they affix a tracking label with a barcode to my package, give me the tracking number associated with the barcode, and every employee who subsequently handles my package (I assume) scans the barcode with a scanner, reporting its whereabouts to a central database that I can consult online in order to track my package through the sequence of location "traces" collected by the database. Employees must not forget to scan my package, the database must work, and the Internet must be available or my tracking activity fails. This empirical tracking amounts to what sociologist Bruno Latour (1999) called establishing a "chain of reference."

Scientists interact with a process by observing ("mental" marking by taking note) or experimenting ("physical" marking by perturbation or alteration) and thereby create "traces": physical remnants that can be used as representations of the state of a marked process at multiple times. A sequence of these traces represents the process as it was tracked. This concept of tracking draws on Salmon's (1984) concept of "mark transmission" as a way of characterizing what it is to be a causal (as opposed to noncausal) process. The idea here is not to rely on Salmon's account as an analysis of causal process, but rather to use it as a characterization of scientific practices of following causal processes by causally interacting with them and using causal interactions as means of detecting, tracking, and individuating processes (Griesemer 2007). Processes that are subject to identity-changing fusions (merging of multiple processes into one) or fissions (splits of one process into several) call for renaming processes by remarking interactions or by relabeling traces so as to track fused and fissioned processes *as* individuals (see Griesemer [2014*a*] on relabeling entities in HIV replication). Differently put, traces only represent processes in so far as they reflect the numerical identity of the process(es) tracked. Reflecting numerical identity in representational, referential use is another way to describe individuation.

Returning to evolutionary individuality and selection processes, Goodnight uses fitness assignment as a way of describing what selection processes are tracked in empirical inquiries into evolution. In operational terms, to receive a fitness assignment is to be given a unique fitness label (a subscript value $i = 1$, or 2, or . . . added to a representation of relative fitness, w), w_i, or to be subjected to a measurement of fitness value, to which a fitness label is given, such that $w_i = \mathrm{w}$. The things that take fitness assignments are the individuals corresponding to selection processes tracked in an empirical study. Evolutionary individuality, in other words, lies in two aspects: (1) the causal intersection of a fitness-assigning process (the scientist) and some biological process (the biological subject/phenomenon) and, prior to that, (2) the individuation of biological processes in a tracking practice performed by the scientist.

I emphasize *assignment* in Goodnight's approach as the lesson to be learned from what went wrong in previous efforts to "solve" the units of selection problem with a definitive *analysis* of that concept or the concept of biological (or evolutionary) individuality. Those attempts had to *presuppose* that to which the properties in play *could* be assigned (replicator, interactor, etc.). Goodnight focuses on the assignment practice itself. He shows that fitness assignment can work as an approach to characterizing evolutionary individuality not because it provides a definitive conceptual analysis, but because it serves a tracking process and practice of individuation. Using Goodnight's definition, one picks out, as the individuals in a contextual analysis (see later discussion), those processes to which fitness had been successfully assigned in a tracking and empirical measurement process. If fitness assignments do not track selection processes—for example, if fitness is assigned to entities that do not vary, or that do not reproduce differentially, or which do not fuse or fission to form fitness-bearing entities in the process(es) tracked—then the empirical results of fitness measurement (in either observation or experiment) may be statistically nonsignificant, so that the fitness assignment failed to track a selection process after all.

In Section 7.4, I consider another approach to the question of evolutionary individuality that is different from, but compatible with, Goodnight's story of fitness assignment. It involves my account of reproducers and how to track them. However, it characterizes processes of reproduction, *with or without* fitness differences or consequences, in a way that can be understood in terms that are far more general than is usual in biology, prior to the problem of units of selection and prior to the tracking problems of fitness assignment and measurement that Goodnight addresses.

Reproduction is a process through which fitness and variation in fitness can be *generated*. “Reproducers” are units with the potential (given the right circumstances) to be potential units of selection (i.e., fitness *bearers* and thus takers of fitness *assignment*), hence they are conceptually and biologically prior to units of selection. By itself, my reproducer approach is abstract and “theoretical,” but it is specified together with a view of how to detect and track reproduction processes beyond the “ordinary” or familiar cases that guide so much of our thinking about candidate units of selection. That is, the concept of a process of reproduction provides insight into the character of biological *individuality* because it is complemented by a tracking practice of *individuation* by means of a “material overlap” criterion for reproductive processes. Material overlap picks out reproduction processes by specifying tracking conditions in ways that help explain why exemplary cases of biological individuality are exemplary and problem cases are problematic. In this way, the concept is heuristic and tied to tracking practice rather than definitional and tied to a conceptual analysis (Griesemer 2014*a*).

Neither Goodnight’s nor my approach need be correct, empirically or theoretically adequate, nor the only ones of their kinds to do the modest illustrative work I aim to do with them in this chapter. The points I want to make are that both approaches, from very different starting points, tie concepts of individuality to particular kinds of empirical processes and both link understanding and interpretation of concepts of individuality to empirical practices of process tracking, either fitness assignment or material overlap. Moreover, with certain additional assumptions, one can view fitness assignment as part of a reproduction process tracking practice or, conversely, view a reproduction process tracking practice as part of a fitness assignment practice, though this further demonstration is beyond the scope of this chapter.

7.3 Goodnight’s Definitions of the (Evolutionary) Individual

Goodnight (2013) entertains the possibility that selection may occur at multiple levels rather than just at the level of organisms and that there might be evolutionary individuals in addition to organisms that are potentially subject to selection at those other levels. His discussion and analysis tacitly assume the primary candidate levels are gene, cell, organism, group (of organisms), species, and multispecies communities. My interest is not in evaluating the argument or evidence for multilevel selection or whether those are the right levels to consider, but rather with Goodnight’s strategy for defining “individual.” His approach involves an interesting blend of theory and practice.

He observes that intuitive concepts of individuality fail to reflect all relevant aspects needed by the science of evolutionary biology, even when considering such canonical organisms as humans. This is because humans only function as organisms because “we” are organized as parts of complex communities or "holobionts" that include mites, skin and gut bacteria, and other, intracellular, symbionts such as mitochondria. Are humans "individual" organisms or communities (Dupré and O'Malley 2009; Gilbert, Sapp, and Tauber 2012; Chiu and Gilbert 2015)? Are intracellular symbionts individuals in their own right or parts? Can individual *organisms* be comprised of other individual *organisms*? In doubting intuitive concepts, Goodnight's approach to individuality is philosophical business as usual: look for problematic cases that challenge orthodoxy and demand conceptual clarification to fit complex reality. But Goodnight also introduces his preferred statistical *method* for analyzing multilevel selection, "contextual analysis," which changes the tenor of the argument for a concept of individuality. Again, my interest is not to defend this method, which is admittedly controversial, nor assess its merits relative to other methods (cf. Lloyd 1988; Okasha 2006). My interest is in how the method suggests an individuation principle for evolutionary individuals and how it is implicated in Goodnight's definitions of individuality.

The background operative idea since the emergence of population genetics in the first half of the twentieth century (Provine 1971) and quantitative evolutionary genetics in the second half (Lande 1976, 1979; Lande and Arnold 1983) is that evolution by natural selection can be interpreted as the operation of a causal process that changes the frequency distribution of genes, genotypes, or phenotypes within a population within a generation and that an evolutionary "response" to selection within generations is due to the transmission of genes or traits between generations (measured by allele frequency change or phenotype "heritability"). One measure of the operation of selection is Price's covariance between relative fitness and phenotype (Price 1970, 1972; Frank 1995; Okasha 2006). Another is the regression of relative fitness on phenotype (Lande and Arnold 1983), discussed by Goodnight (2013).

Contextual analysis extends standard regression analysis to represent effects of "context" on variables measured at a focal level (Heisler and Damuth 1987). For example, if phenotypic traits of organisms in a population are measured along with some measure of organism fitness (e.g., number of progeny), a standard way to assess selection is to calculate the statistical regression of relative fitness on phenotype. When regression coefficients in this sort of analysis are statistically significantly different than 0 (i.e., the fitness surface has non-zero slope), that is taken as evidence that selection is operating. But operating on what? In the case as described, it is operating on organisms, the things to which fitness and phenotype values are assigned and thus have been (or could be) measured.

If the population is a "meta"-population subdivided into multiple "sub"-groups, however, then there might be an effect on organism phenotype of membership in a particular *group* or an effect on organism phenotype due to selection operating on groups themselves. Contextual analysis adds to the calculation group phenotypes, as described in a meta-population story, allowing representation of these "contextual effects" by computing and comparing partial regression of fitness on both individual phenotype and on group mean phenotype. If group phenotype is a statistical function of individual phenotypes (e.g., average individual phenotype within each group), that is called a "composite variable" (Goodnight 2013: 38), which can be used to identify a group effect on individual phenotype. If a group phenotype that is *not* a function (or not the right sort of function) of individual phenotype is also measured—that is, a "contextual variable" such as population size or emigration rate (which cannot be assigned to individual organisms but can be assigned to groups as wholes)—then a contextual analysis can show that group selection is operating by detecting a significant regression of fitness on *group-level trait* (Goodnight 2013: 39, cf. box 2.1). For my purposes, further details of the method are not important. I draw attention to some key implications of the method for individuation and individuality.

First of all, contextual analysis admits of only one level for fitness assignment. The other level considered in the analysis is a context for the focal level. In the examples Goodnight (2013) considers, these levels resolve to organism (individual) and group (context). It does not follow that contextual analysis can only discover, display, or represent fitness at the level of assignment, however. As Goodnight points out, the discovery that some measured variables are "contextual" rather than "composite" provides evidence that selection operates at the group level and thus that, although investigators may have assigned (and tracked) fitness at the organism level in a particular study, they could have assigned, modeled, and tracked fitness at what in this study is group level because the analysis revealed that there is a significant causal process of selection operating at that level. Thus, fitness *assignment* is a function of investigator interest, ability, and opportunity and a matter of investigator choice. It is part of a practice of empirical measurement, which contextual analysis represents in particular respects. In some of the examples Goodnight describes (e.g., paleontological studies of fossil species or higher taxa), there is no doubt that paleontologists believe organisms in populations within species vary in fitness, but there is seldom opportunity for paleontologists to measure those fitness differences in fossils, so paleontologists do not assign fitness below the level of species because (typically) they cannot measure it: they cannot get the data; they cannot track the process operating at that level.

Second, because contextual analysis describes and represents selection at a particular focal level of measurement chosen by the investigator and admits discovery of composite and contextual effects at higher levels, processes operating *below* the focal level are not *described* as selection processes because the analysis does not track or evaluate *fitness* below the focal level. Because fitness is not *assigned* at any lower level than the focal level, processes operating below the focal level must be described as something else. Goodnight suggests that these processes are typically described as developmental rather than selective:

> [C]hanges at or above the level at which fitness is assigned can be described in terms of evolution and natural selection. This is because there is variation among units for the level at which fitness is assigned, and changes at

> or above this level can be described in terms of fitness differences. Below the level at which we assign fitness, such distinctions are not possible, since all entities that make up one of the units for which we define fitness by definition have the same fitness. Therefore, we have to use another term for changes taking place below the level at which fitness is assigned. Thus, for example, it is customary to assign fitness at the level of the organism, and changes in phenotype at the organismic level or higher can be described in terms of evolution. Below the level of the organism, we cannot describe changes in terms of evolution, and instead use the term *development* to describe changes within the organism. (Goodnight 2013: 39)

If we can fairly characterize changes in context above the focal level at which fitness is assigned as "ecological," then we get the following picture: contextual analysis describes selection operating at a focal level at which fitness is assigned. Above that level, ecological processes operate through "composite" variables that may have effects on the focal level (so-called multilevel selection 1 or MLS1) and selection processes have effects on the group level that can be detected at the focal level through "contextual" variables (so-called multilevel selection 2 or MLS2).[4] Below the focal level, developmental processes operate that play a constitutive role in the generation of units at the focal level. It may be that, below focal level, selection processes do operate, but the choice to assign (and measure) fitness at the focal level forces description of those processes as developmental. It may be that above focal level, selection processes operate, but the choice to assign (and measure) fitness at the focal level forces description of those processes as ecological. Yet the discovery that some of those ecological processes operate through contextual (rather than composite) variables indicates selection may be occurring at the ecological level, and a full understanding of selection would thus require further work to represent, assign, and measure fitness at that contextual level by taking population structure explicitly into account (see also Lloyd 2001).

If evolutionary individuality is understood as that to which fitness is assigned, Goodnight's first definition of the individual (p. 42), then "the concept of 'individuality' is an artificial construct imposed by the observer" (Goodnight 2013: 48). By that, I take it, Goodnight means that "the individual" is imposed in the analysis by the choice of fitness assignment, not that the reality of what causal *processes* operate in the world are constructed by the investigator. His is not a *pernicious* relativism, but rather a process relativity of concept to what it is of interest to the investigator to track by assigning and measuring fitness in a particular way. To give it a philosophical label, we might call this a "process realism with entity (or level) relativism" or simply "processualism." Or, eschewing metaphysics, we could say that Goodnight identifies the "logical individuals" or "units of analysis" in a

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[4] Note that Goodnight considers the MLS1/MLS2 distinction misleading. See Heisler and Damuth (1987), Damuth and Heisler (1988), for the origins of this distinction. See Okasha (2006) for a review.

contextual analysis as those units to which fitness is assigned and measured. As Goodnight goes on to say:

> [T]here is no one level that can clearly be called "the individual" to the exclusion of other levels. One level may be the individual with respect to one selective force, and in the same system a different level may be the individual with respect to a different selective force, and finally, the investigator may choose yet a third level of organization to define as the individual. (Goodnight 2013: 49)

In Goodnight's picture, processes within organisms might be selection processes (e.g., cancers might be selection processes operating at cellular level) but, due to the organization of those organisms in which there is a cellular bottleneck in the production of germ cells, somatic cell cancers only rarely exhibit evolutionary responses to selection beyond the reproductive generation of the organisms that suffer them. Thus, for practical reasons, it rarely is of value or interest to assign and measure fitness at cell rather than organism level and thus more effective to interpret cancer as a developmental than a selective process. That does not preclude studying cancer as a within-body selection process, but it does explain why it is impractical to do so for studies that focus on other levels.

In the interest of full understanding of selection in a particular system, we would perhaps, Goodnight argues, want to consider a definition of the individual as the unit of analysis (that which takes fitness assignment) at the *lowest* level at which selection is *actually* acting (Goodnight's definition 2, p. 44), rather than at a *focal* level of investigator interest. This would facilitate discovery, through contextual analysis, of all levels above the lowest at which selection is acting through the detection of contextual effects operating through contextual variables. This definition still relies on the notion of fitness assignment to units at a level as the core concept of individuality, or rather, principle of individuation. However, for empirical reasons (evolutionary response is presumed rare below organism level) and practical reasons (fitness and selection response measurement below organism level is hard), the value repaid in research results is rarely worth the effort required. It is cheaper, faster, better to pick a promising focal level than to start at "the bottom" of a presupposed hierarchy of levels and assign/measure fitness all the way up, "just in case." A theoretician's reply to this pragmatic strategy is: "How do you know evolutionary response below organism level is rare unless you test for it?" The same critique applies to measurement above organism level in deciding whether to test for population structure.

Goodnight's third definition—the individual is (a unit at) the lowest level at which a *response* to selection can occur (p. 47)—does not add to the points I want to make about individuation in practice, so I shall set consideration of it aside for present purposes.

The methodological commitment to track individuality through fitness assignment at a focal level, as required by contextual analysis, relegates to "development" those processes occurring below the focal level. This is a concept of development needed for *evolutionary* explanation. What about development as needed for *developmental* explanation "at" a focal level? Even though organisms are typically "the individuals" assigned fitnesses in evaluations of evidence of the operation of selection, whether through contextual, regression, or covariance analysis, it is also the case that organisms—the entities at the conventional focal level—develop (and reproduce, metabolize, behave, and interact ecologically). Organisms are not *mere* fitness bearers engaged only in selection processes "at their own level." They may be individuated with respect to other processes in addition to selection. Fitness assignment and methodological commitment to use contextual analysis may support ontological commitment to certain sorts of *evolutionary* individuals (assuming the empirical evidence is favorable), but that does not preclude other practices and methodological commitments for tracking other sorts of processes at organism level or any other level. Goodnight acknowledges that selection may operate at multiple levels, which leads to a process-relative, pluralistic perspective, but we should also acknowledge that other kinds of processes might operate "at" a level and simultaneously at multiple levels unless there are special reasons differentiating kinds of processes in this particular respect regarding levels of organization.

Moreover, if it is the case that to be a fitness bearer, to take a fitness assignment at a level, the individual must also be an individual with respect to processes other than selection, it may be that to have the potential to be an evolutionary individual, an entity or process may need to have the potential to be an individual with respect to those other processes. Thus, the potential to take a fitness assignment might be understood as the potential (in virtue of those other processes) to have the potential to take a fitness assignment. If that is the way things are, then it would seem that evolutionary individuality rests, conceptually, on other forms of individuality.

In the next section, I sketch an account of reproduction supporting a concept of "developmental individuality." I also suggest a tracking criterion for developmental individuality—material overlap—that demarcates developmental and reproductive "generations" and thus serves as an individuation criterion.

7.4 Reproducers and Reproductive Individuality

My purpose in this section is not to defend my account of reproducers (Griesemer 2000*a*, 2000*b*, 2000*c*, 2002, 2005, 2006*a*, 2014*a*, 2014*b*, 2016), but to use it, as in the previous section, as an example of an account of concepts supporting a notion of evolutionary individuality linked to a concept of individuation. As in the previous section, a focus on biological processes together with a tracking procedure and criterion of individuation leads to a "process realism with entity relativism" or "processualism." Here, the process is reproduction (and a recursively entwined process, development) rather than selection.[5] The tracking procedure is to look for "material overlap" relations and to relabel what is tracked each time a certain kind of fission or fusion event among processes, called a "scaffolding interaction," occurs, rather than to track whatever receives a fitness assignment, as in Goodnight's account. This relabeling practice delimits or individuates processes as biological individuals (reproducer or developer individuals) that have the potential to be potential units of selection. Thus, an evolutionary individual is a trackable reproducer process with the potential to be a potential unit of evolution (or selection).

However, the account also blurs lines between what conventionally count as reproduction and development processes, revealing a new problem of individuation *of generations* that is fundamental for a generalized population biology and thus for an extended theory of evolution. Like Goodnight's fitness assignment and contextual analysis, what lies below (above) a focal level of reproduction is development (ecology), but that lower level of development can be focal-level reproduction in its own right with a developmental (ecological) level below (above) that. Unlike Goodnight's fitness assignment approach, however, the reproducer account's individuation criterion—material overlap through scaffolding interactions—does not have the inherent asymmetry of fitness assignment at focal levels because it does not depend on a concept of statistical variation (at a level) that by definition disregards variation at lower levels.

The motivation is threefold, to (1) emphasize the materiality of reproduction rather than the abstract, informational properties of genes and replication; (2) reconnect problems of heredity and development after they were sundered in twentieth-century conceptual dichotomies like auto-/hetero- catalytic functions of DNA, gene transmission/expression, and genotype/phenotype; and (3) characterize the process of reproduction in terms that do not themselves require evolutionary analysis to avoid the circularity problems discussed earlier.

Maynard Smith (1987), in considering where to place Malthus's principle in relation to Darwin's, noted that the entities subject to evolution (and its special case: evolution by means of natural selection) must *multiply*. Whether Malthus's principle is a law of nature or merely a likely condition in which population growth tends to outstrip food supply is less important than the constraint on Darwin's principles to apply to things which multiply. I interpret the multiplication condition in Maynard Smith's principles of evolutionary units as a principle of reproduction (Griesemer 2000*c*). That is, evolution operates on "reproducers," or, more precisely, evolutionary processes are a special class of reproduction processes.

Evolution can be understood as descent with modification of a population of "reproducers." Reproduction is multiplication (of processes or entities) with material overlap conveying developmental capacities (i.e., material propagule

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[5] On process entwinement, see Griesemer (2007).

generation or "pro-generation"). Material overlap means that at least some material parts of the "offspring" were formerly material parts of the "parents." Thus, reproduction involves a bond of material continuity, not merely one of resemblance or formal transmission of information. If material can be suitably marked through causal interaction, it can be tracked. So, the material overlap condition in the characterization of reproduction also yields a tracking criterion. Materials which "track together" can be counted an individual for a purpose of study.

To count as reproduction, rather than mere duplication or copying, at least some materially overlapping parts must convey developmental capacities to offspring (Griesemer 2000*a*, 2014*a*, 2014*b*, 2016). Development is the recursive acquisition (or refinement) of a capacity to reproduce. Recursion bottoms out in "null development"—progenerated entities originate with a capacity to reproduce, rather than having to acquire it by exercise of developmental capacities. Development in the special case of multicellular organisms, for example, requires reproduction of cells, reproduction of cells requires development of cellular capacities, and cell development requires chemical autocatalysis (null development) of cellular constituents. There is no fixed, asymmetrical relation between reproduction and development via material overlap as there is between selection and development (or ecology) in Goodnight's fitness assignment criterion of individuality. Although contextual analysis can shift focal levels, it must do so in order to treat a given level as selection rather than development. The reproducer account allows a plurality of interpretations of processes at each level as either development or reproduction, *depending on the choice of what material overlap relations to track at that level* because reproduction and development are mutually embedding processes at each level.

If one looks at the details of development, at any level of organization, one finds processes that look materially like reproduction: material processes fuse and fission; in the hybrid, fused state transformations take place that constitute acquisition of new developmental capacities; exercise of those capacities facilitates transition to a new developmental state, perhaps involving further fusions or fissions. Clearly, development of multicellular organisms involves reproduction by fissioning of cells as well as aggregation and differentiation (fusion in a different sense than fertilization) of cells interacting in weak to tight cell junctions to form organized tissues and organs. If we were to track these fusions, fissions, and transformations with cells, or even molecules, rather than organisms as the entities filling the roles of parents and offspring, it would be tempting to treat the fusion and fission events as *reproductive* processes in complex life cycles delimiting reproducers at a lower level than organisms, with many "developmental generations" separating reproductive generations (Griesemer 2016), just as cell generations mark developmental stages of the reproductive generations of multicellular organisms.

Griesemer (2014*a*) argues that (complex) molecules, such as HIV retrovirus genomes, *develop* and that hybrid complexes of them with various proteins *reproduce*, all within the span of a single host cell's life cycle. Griesemer (2016) argues that this and other cases indicate an important sense in which all life cycles are complex and that what is often called "development" can be evaluated as reproduction by tracking material overlap relations among the fusing and fissioning entities. The complexity of life cycles can be interpreted as due to transitions in the "ecological" contexts of development, marked by certain sorts of developmental interactions with elements of a developmental environment. Complex life cycles are not solely the province of parasites with multiple hosts.

One further concept completes the picture of reproduction: developmental scaffolding. Most developmental processes are facilitated rather than autonomous in the sense that the aid of an "external" process interacting with the developing system makes easier, or more likely, or with lower fitness cost, the acquisition, refinement, or exercise of a new developmental capacity (Caporael, Griesemer, and Wimsatt 2014). I say "external" because, on traditional accounts of compositional levels of organization, the scaffold is one thing, the thing scaffolded is another thing, and the pair in interaction may or may not be treated as a thing at a higher level. A human parent may scaffold a child to learn to cross the street safely—a capacity that can only be acquired after a certain state of cognitive development has been attained by the child and a certain state of cognitive maturity has been attained by the parent. To say that the child is our focal unit of development and the parent is part of the environment or ecological context of child development, albeit a very special one, is to track the material relations within the child over time and place without regard for the material relations between parent and child. In a sense, we commit to the child as an individual before the interaction, as an individual after the interaction, and as the same individual spanning the interaction, though perhaps changed in properties and capacities. From the point of view of focal interest in the child, little or no commitment is made to the ontological status of the parent. If attention does shift to her, then similar considerations apply.

A different view in keeping with the reproducer perspective (Griesemer 2014*a*, 2014*b*, 2016) is that the parent and child form a hybrid process by their temporary fusion (e.g., by holding hands), *intra*-action (tugging, guiding, pulling, and also talking, pointing out, exclaiming) as parts of a whole in a street-crossing phase, and fission (letting go hands) on the other side of the street.[6] In other words, the child and parent form a new individual due to their developmental interaction that "fuses" them in a psychosocial sense, a social developmental individual that persists for a short while, and then fissions into two more autonomous individuals after their interaction. This hybrid, dyadic individual is itself composed of individuals—the child and the parent; they do not lose their individuality (in that they can be tracked through the interaction), though they each cede a measure of autonomy for the duration of the interaction. Hybridization of this kind is the

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[6] I take the concept of "intra-action" from Barad (2007).

formation of a new entity—a new individual—by fusion. Separation marks the formation of two entities from one.

For a variety of reasons, we are typically inclined to individuate and track with proper names or labels the parent as numerically the same parent and the child as numerically the same child who entered the street-crossing episode and exited it and to think of the pair as a mere temporary association of separate, distinct, more-or-less autonomous individuals and to discount claims that the dyad is itself an individual. Chief among these reasons is that when we track material relations, we tend not to regard material relations as an aspect of social relations nor to think of the temporal relations as well as the spatial relations when we note that the parent and child did not "exchange" any significant material parts with one another; there is no material overlap between *them* in the street-crossing episode. But there is material overlap between the child pre–street-crossing experience and the parent–child pair, and between the parent–child pair and the child post–street-crossing experience. The same holds for the parent. The fact that each emerges with more or less the same overall structure and properties as they entered the hybrid makes this social learning interaction *more* like semi-conservative DNA replication rather than less (Griesemer 2014*a*).

In general, the reproducer perspective suggests that a developmental individual be understood as a reproductive process individuated and marked, from start to finish, by developmental scaffolding interactions. Each time new developmental capacities are gained through hybrid-forming scaffolding interactions (in a process-relative sense specific to the kinds of scaffolds and developers causally interacting) or exercised in ways that result in new scaffolding interactions, we can recognize fusions and fissions in a material sense that mark off distinct "developmental generations" within a life cycle delimited by progeneration events demarcating "reproductive generations" (Figure 7.1A). In a similar vein, Salmon (1984) recognized that each pair of causal intersections, no matter how brief or seemingly insignificant, delimited distinct causal processes. However, although this means that a hit baseball traveling from the bat that strikes it to the window it breaks is "really" a sequence of many processes (as the ball also interacts with many molecules in the air on the way to the window), for many practical purposes, we discount these interactions and concatenate the many elemental component processes into a single struck-baseball process.

While we need not regard distinct developmental generations as delimiting numerically distinct *organisms* or reproducers (any more than metamorphosis marks the tadpole as one organism and the frog as another), we can consider that scaffolding events give us another way to interpret the organization of developmental processes into temporal sequences comprising higher level individuals in a way analogous to cell generations marking developmental stages of a multicellular, higher level individual organism. Since scaffolding in development creates new hybrid material entities through which new developmental capacities can be acquired, and conveyance of developmental capacities is the characteristic of

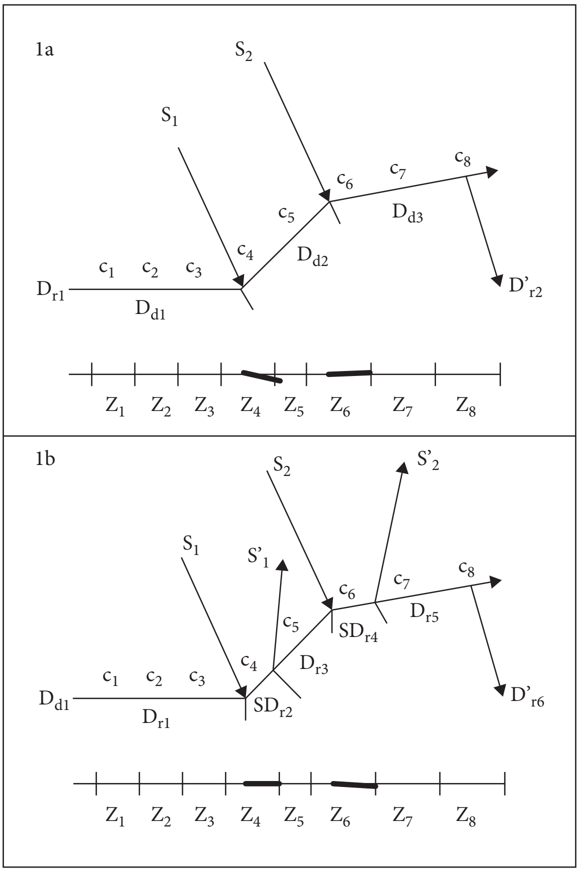

FIGURE 7.1 *Scaffolded development and reproduction.* **A**: *Traditional interpretation of development in which reproduction results in numerically distinct, spatially individuated reproducers. The transitions between reproductive generations (r1, r2) are marked by developmental stages (d1, d2, d3). Z is a Vygotskian zone of proximal development (see Caporael, Griesemer, and Wimsatt 2014)—a window in which the developer is capable of acquiring a new skill or capacity. D is a developmental process (indicated by the bent arrow running from left to right), subscripted r1 for the "parent" reproductive generation. D′ is its reproductive offspring in generation r2. In between, in the development of D, new capacities* c_i *(i = 1 to 8) are acquired and exercised. S is a scaffold that interacts (causal arrow intersecting the causal arrow of D) at a particular time in development. Here,* S_1 *scaffolds D in a scaffolding interaction with onset in zone* Z_4 *and continuing to the end of* Z_4*, at which time D has acquired* c_4 *which is necessary for D to acquire* c_5*, which facilitates interaction with scaffold* S_2*. Thick bars on the developmental time line show the duration of scaffolding interactions in* Z_4 *and* Z_6*.* **B** *is similar to* **A** *except each developmental "stage" in* **A** *called a "developmental generation" (d1, d2, d3) is here called a "reproductive generation" to note the material overlap relations between* D_{r1}*,* SD_{r2}*,* D_{r3}*,* SD_{r4}*,* D_{r5}*, and* D'_{r6}*.* SD_{r2} *and* SD_{r4} *denote hybrid entities formed by the fusion of a scaffold, S, and developer, D. (Development of the scaffolds not shown.) D and S in generation r1 are "parents" of the hybrid offspring SD in generation r2. SD is the "parent" of offspring S1 and D in r3. And so forth.*

material reproduction processes, how we choose to mark, track, and measure material overlap relations amounts to the constructed aspect of reproductive and developmental individuality on par with Goodnight's constructed aspect of evolutionary individuality via fitness assignment. We can, in other words, interpret scaffolding interactions as delimiting developmental individuals and the markable material that passes through them as assignable to distinct developmental or reproductive generations (compare Figures 7.1A and B). In Figure 7.1A, three "developmental generations" separate two reproductive generations. In Figure 7.1B, six reproductive generations are separated by scaffolding interactions. The latter concept is analogous, but more fine-grained, to saying that human parents are really grandparents of their children: they form gametes as their immediate offspring; gametes are the parents that fuse to form a zygote, or grand-offspring (Griesemer 2014*a*, 2016).

On this kind of processualism, an *organism* is a construct depending on investigator interest in and tracking ability for certain kinds of reproducers, together with the reproducer and developer capacities of the processes tracked. These developmental individuals and generations can be tracked and delimited by marking developing processes that hybridize with scaffolds. They can be remarked or relabeled when they form new hybrid individuals constituting a new developmental or reproductive generation (depending on tracking interest) and relabeled again when constituting a third generation after scaffolds and developers separate (Figure 7.1B). Marking, tracking, and relabeling material that enters or exits a reproduction process delimited in a number of developmental or reproductive generations does not depend on tracking statistical variation in a population of processes, so tracking material overlap relations does not carry the same sort of asymmetry between levels that Goodnight's fitness assignment tracking does. There are still focal choices, but here they are not dictated by a relation between levels of organization but rather by a choice between what to track and what not to track.

7.5 Individuality as a Partial Ordering Rather than Degree Property

One further implication of this view suggests an alternative to treating individuality as a degree property tuned by the value of several parameters in a cooperation/conflict model, as in Queller and Strathmann's approach and as examined in depth by Godfrey-Smith (2009) in his Darwinian spaces model that maps the menagerie of reproductive modes in the three dimensions of cellular bottlenecks, germ–soma specialization, and integration. I have argued that individuality can be understood in terms of tracking material overlap relations—the analog of tracking fitness assignment in Goodnight's contextual analysis of statistical variation in populations. I also suggested that this notion of individuality is process-relative: individuality depends on individuation that happens in marking and tracking choices relative to a process of interest. Because of this process-relativity and the evident multitude of processes that can interact, we can think of the "degree property" of individuality rather as a partial ordering relation of "orders of individuality."

An individual is "stronger," more robust, when more processes track together than when fewer track together. If a marking interaction can be used to track material overlap relations with respect to several processes, it individuates a stronger individual than if it tracks only a subset of those processes. Vertebrate organisms strike us as very coherent, cohesive, "strongly" individual in part because the cellular parts of vertebrates seldom go their separate ways such that a variety of biological processes of interest (from physiology to behavior, development to reproduction, to ecological interaction) have to be tracked separately. Not so with a cellular slime mold, whose cellular parts can go their separate spatial ways and still be "one organism." In the case of sponges, the separate parts can come back together after being disaggregated, so we think of the period of separation (perhaps at the hands of an experimenter) as merely a stage in the peculiar developmental history of "the" sponge. Sponges and slime molds are weaker individuals than we are because their looser need for spatial contiguity of parts means we cannot track the "whole" organism by, say, marking the genome of a single stem cell. That would do for a vertebrate.[7] The holobiont perspective raises new questions not only about the individuality of the human organism, but about the salient tracking criteria for such entities. If humans plus their microbiomes are holobionts with a similarly distributed "hologenome" (Gilbert et al. 2018), then tracking humans through reproductive generations by tagging genes of the *Homo sapiens* component of human holobionts is inadequate unless microbiome transmission is strictly "vertical."

The notion that individuality can be partially ordered relative to a set of trackable processes of interest suggests a way of extending this processualism to other sciences. I have focused on reproduction and development because I believe these are fundamental to biological problems of evolution and, indeed, the evolution of biological individuality. But the view may be more general. What we take to be individuals rests in part on our ability to mark and track processes of interest, and, to the extent that many trackable processes "track together," we find individuals.

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[7] Modulo the skin cells we tend to slough off and thus not *count* as part of the body any longer. In that case, our strong-individual marking/tracking criterion would fail when we happened to mark the genome of that skin cell. Thanks to Melinda Fagan for stressing that, even for vertebrates, marking some body cells will not do to track vertebrates throughout their life trajectories unless it is a stem cell that is marked.

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References

Antonovics, Janis, Norman Ellstrand, and Robert Brandon. 1988. Genetic variation and environmental variation: expectations and experiments. In *Plant evolutionary biology*, eds. Leslie Gottlieb and Subodh Jain, 275–303. New York: Chapman and Hall.

Barad, Karen 2007. *Meeting the universe half way: Quantum physics and the entanglement of matter and meaning*. Durham, NC: Duke University Press.

Bonner, John T. 1952. *Morphogenesis: An essay on development*. Princeton: Princeton University Press.

Bonner, John T. 1967. *The cellular slime molds*, 2nd ed., revised and augmented. Princeton: Princeton University Press.

Bouchard, Frédéric, and Philippe Huneman (eds.). 2013. *From groups to individuals: Evolution and emerging individuality*. Cambridge, MA: MIT Press.

Buss, Leo W. 1987. *The evolution of individuality*. Princeton: Princeton University Press.

Caporael, Linnda, James Griesemer, and Willam Wimsatt (eds.). 2014. *Developing scaffolds in evolution, culture, and cognition*. Cambridge, MA: MIT Press.

Chiu, Linn, and Scott Gilbert. 2015. The birth of the Holobiont: Multi-species birthing through mutual scaffolding and niche construction. *Biosemiotics* 8: 191–210.

Clarke, Ellen 2010. The problem of biological individuality. *Biological Theory* 5(4): 312–325.

Damuth, John, and Ida L. Heisler. 1988. Alternative formulations of multilevel selection. *Biology and Philosophy* 3: 407–430.

Dawkins, Richard. 1976. *The selfish gene*. New York: Oxford University Press.

Dawkins, Richard. 1982. *The extended phenotype: The gene as the unit of selection*. New York: Oxford University Press.

Dobzhansky, Theodosius. 1973. Nothing in biology makes sense except in the light of evolution. *American Biology Teacher* 35(3): 125–129.

Dupré, John, and Maureen O'Malley. 2009. Varieties of living things: Life at the intersection of lineage and metabolism. *Philosophy and Theory in Biology* 1: e003.

Frank, Steven A. 1995. George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology* 175: 373–388.

Gánti, Tibor. 2003. *The principles of life, with a commentary by James Griesemer and Eörs Szathmáry*. Oxford: Oxford University Press.

Gilbert, Scott, and David Epel. 2009. *Ecological developmental biology*. Sunderland: Sinauer Associates.

Gilbert, Scott, Eugene Rosenberg, and Ilana Zilber-Rosenberg. 2018. The Holobiont with its hologenome is a level of selection in evolution. In *Landscapes of collectivity in the life sciences*, eds. Snait Gissis, Ehud Lamm, and Ayelet Shavit, 305–324. Cambridge, MA: MIT Press.

Gilbert, Scott, Jan Sapp, and Alfred Tauber. 2012. A symbiotic view of life: We have never been individuals. *Quarterly Review of Biology* 87: 325–341.

Godfrey-Smith, Peter. 2009. *Darwinian populations and natural selection*. New York: Oxford University Press.

Godfrey-Smith, Peter. 2013. Defining individuals. In *From groups to individuals: Evolution and emerging individuality*, eds. Frédéric Bouchard and Philippe Huneman, 17–36. Cambridge, MA: MIT Press.

Goodman, Nelson, and Henry S. Leonard. 1940. The calculus of individuals and its uses. *Journal of Symbolic Logic* 5: 45–55.

Goodnight, Charles J. 2013. Defining the individual. In *From groups to individuals: Evolution and emerging individuality*, eds. Frédéric Bouchard and Philippe Huneman, 37–53. Cambridge, MA: MIT Press.

Griesemer, James. 1994. Tools for talking: Human nature, Weismannism and the interpretation of genetic information. In *Are genes us? The social consequences of the new genetics*, ed. Carl Cranor, 69–88. New Brunswick: Rutgers University Press.

Griesemer, James. 2000*a*. Development, culture and the units of inheritance. *Philosophy of Science* 67 (Proceedings): S348–S368.

Griesemer, James. 2000*b*. Reproduction and the reduction of genetics. In *The concept of the gene in development and evolution: Historical and epistemological perspectives*, eds. Peter Beurton, Raphael Falk, and Hans-Jörg Rheinberger, 240–285. New York: Cambridge University Press.

Griesemer, James. 2000*c*. The units of evolutionary transition. *Selection* 1: 67–80.

Griesemer, James. 2002. Limits of reproduction: A reductionistic research strategy in evolutionary biology. In *Promises and limits of reductionism in the biomedical sciences*, eds. Marc H. V. Van Regenmortel and David Hull, 211–231. Chichester: John Wiley and Sons.

Griesemer, James. 2005. The informational gene and the substantial body: On the generalization of evolutionary theory by abstraction. In *Idealization XII: Correcting the model, idealization and abstraction in the sciences (Poznan studies in the philosophy of the sciences and the humanities, volume 86)*, eds. Martin Jones and Nancy Cartwright, 59–115. Amsterdam: Rodopi.

Griesemer, James. 2006*a*. Genetics from an evolutionary process perspective. In *Genes in development*, eds. Eva M. Neumann-Held and Christoph Rehmann-Sutter, 199–237. Durham, NC: Duke University Press.

Griesemer, James. 2006*b*. Theoretical integration, cooperation, and theories as tracking devices. *Biological Theory* 1(1): 4–7.

Griesemer, James. 2007. Tracking organic processes: Representations and research styles in classical embryology and genetics. In *From embryology to evo-devo: A history of developmental evolution*, eds. Manfred Laubichler and Jane Maienschein, 375–433. Cambridge, MA: MIT Press.

Griesemer, James. 2008. Origins of life studies. In *The Oxford handbook of philosophy of biology*, ed. Michael Ruse, 263–290. New York: Oxford University Press.

Griesemer, James. 2013. Formalization and the meaning of "theory" in the inexact biological sciences. *Biological Theory* 7: 298–310.

Griesemer, James. 2014*a*. Reproduction and the scaffolded development of hybrids. In *Developing scaffolds in evolution, culture, and cognition*, eds. Linnda Caporael, James Griesemer, and William Wimsatt, 23–55. Cambridge, MA: MIT Press.

Griesemer, James. 2014*b*. Reproduction and scaffolded developmental processes: An integrated evolutionary perspective. In *Towards a theory of development*, eds. Alessandro Minelli and Thomas Pradeu, 183–202. New York: Oxford University Press.

Griesemer, James. 2016. Reproduction in complex life cycles: A developmental reaction norms perspective. *Philosophy of Science* 83: 803–815.

Griesemer, James, and Michael J. Wade. 1988. Laboratory models, causal explanation and group selection. *Biology and Philosophy* 3: 67–96.

Guay, Alexandre, and Thomas Pradeu (eds.). 2016. *Individuals across the sciences*. Oxford: Oxford University Press.

Heisler, Ida L., and John Damuth. 1987. A method for analyzing selection in hierarchically structured populations. *American Naturalist* 130: 582–602.

Hull, David. 1980. Individuality and selection. *Annual Reviews of Ecology and Systematics* 11: 311–332.

Hull, David. 1981. The units of evolution: A metaphysical essay. In *The philosophy of evolution*, eds. Uffe Jensen and Rom Harré, 3–44. Brighton: Harvester Press.

Hull, David. 1988. *Science as a process*. Chicago: University of Chicago Press.

Jackson, Jeremy, Leo Buss, and Robert Cook (eds.). 1985. *Population biology and evolution of clonal organisms*. New Haven: Yale University Press.

Kauffman, Stuart. 1993. *The origins of order: Self-organization and selection in evolution.* New York: Oxford University Press.

Lande, Russell 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30: 314–334.

Lande, Russell. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. *Evolution* 33: 402–416.

Lande, Russell, and Stevan J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.

Latour, Bruno. 1999. *Pandora's hope: Essays on the reality of science studies.* Cambridge, MA: Harvard University Press.

Lewontin, Richard. 1970. The units of selection. *Annual Review of Ecology and Systematics* 1: 1–17.

Lloyd, Elisabeth A. 1988. *The structure and confirmation of evolutionary theory*. New York: Greenwood Press.

Lloyd, Elisabeth A. 2001. Units and levels of selection: An anatomy of the units of selection debates. In *Thinking about evolution: Historical, philosophical, and political perspectives,* vol. 2, eds. Rama S. Singh, Costas B. Krimbas, Diane B. Paul, and John Beatty, 267–291. New York: Cambridge University Press.

Lloyd, Elisabeth A. 2012. Units and levels of selection. *The Stanford encyclopedia of philosophy* (winter 2012 edition), ed. Edward N. Zalta. Accessed October 29, 2016. http://plato.stanford.edu/archives/win2012/entries/selection-units/.

Malthus, Thomas R. 1826. *An essay on the principle of population*. London: John Murray.

Maturana, Humberto, and Francisco Varela. 1980. *Autopoiesis and cognition: The realization of the living*. Boston studies in the philosophy of science volume 42. Boston: D. Reidel.

Maynard Smith, John. 1987. How to model evolution. In *The latest on the best: Essays on evolution and optimality*, ed. John Dupré, 119–131. Cambridge, MA: MIT Press.

Maynard Smith, John, and Eörs Szathmáry. 1995. *The major transitions in evolution*. Oxford: W. H. Freeman Spektrum.

Mayr, Ernst. 1961. Cause and effect in biology. *Science* 134(3489): 1501–1506.

McFall-Ngai, Margaret, Michael G. Hadfield, Thomas C. G. Bosch, Hannah V. Carey, Tomislav Domazet-Lošo, Angela E. Douglas, et al. 2013. Animals in a bacterial world: a new imperative for the life sciences. *Proceedings of the National Academy of Sciences USA* 110(9): 3229–3236. doi: 10.1073/pnas.1218525110. Epub Feb. 7, 2013.

Michod, Richard. 1999. *Darwinian dynamics: Evolutionary transitions in fitness and individuality*. Princeton: Princeton University Press.

Moorad, Jacob A., and Michael J. Wade. 2013. Selection gradients, the opportunity for selection, and the coefficient of determination. *American Naturalist* 181(3): 291–300.

Moreno, Alvaro, and Matteo Mossio. 2015. *Biological autonomy: A philosophical and theoretical enquiry*. History, philosophy and theory of the life sciences, volume 12. New York: Springer.

Okasha, Samir. 2006. *Evolution and the levels of selection*. Oxford: Oxford University Press.

Pigliucci, Massimo, and Gerd Müller (eds.). 2010. *Evolution: The extended synthesis*. Cambridge, MA: MIT Press.

Price, George R. 1970. Selection and covariance. *Nature* 227: 520–521.

Price, George R. 1972. Extension of covariance selection mathematics. *American Journal of Human Genetics* 35: 485–490.

Provine, William. 1971. *The origins of theoretical population genetics*. Chicago: University of Chicago Press.

Queller, David, and Joan Strathmann. 2009. Beyond society: The evolution of organismality. *Philosophical Transactions of the Royal Society B* 364: 3143–3155.

Ruiz-Mirazo, Kepa, and Alvaro Moreno. 2012. Autonomy in evolution: From minimal to complex life. *Synthese* 185: 21–52.

Salmon, Wesley. 1984. *Scientific explanation and the causal structure of the world*. Princeton: Princeton University Press.

Sober, Elliott. 1984. *The nature of selection*. Cambridge, MA: MIT Press.

Sober, Elliott, and David S. Wilson. 1998. *Unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University Press.

Strawson, Peter F. 1959. *Individuals: An essay in descriptive metaphysics*. London: Methuen.

Sultan, Sonia. 2015. *Organism and environment: Ecological development, niche construction, and adaptation*. New York: Oxford University Press.

Wade, Michael J. 1976. Group selection among laboratory populations of *Tribolium*. *Proceedings of the National Academy of Sciences* 73(12): 4604–4607.

Wade, Michael J. 1977. An experimental study of group selection. *Evolution* 31: 134–153.

Wade, Michael J. 2016. *Adaptation in metapopulations: How interaction changes evolution*. Chicago: University of Chicago Press.

Wagner, Günter. 2014. *Homology, genes, and evolutionary innovation*. Princeton: Princeton University Press.

Waters, C. Kenneth. 2008. How practical know-how contextualizes theoretical knowledge: Exporting causal knowledge from laboratory to nature. *Philosophy of Science* 75: 707–719.

Wiggins, David. 1980. *Sameness and substance*. Cambridge, MA: Harvard University Press.

Wimsatt, William. 1980. Units of selection and the structure of the multi-level genome. *PSA 1980 Volume Two: Symposia and Invited Papers* 47(2): 122–183.