CHAPTER 6 | What Biofilms Can Teach Us about Individuality

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6.1 Introduction

This chapter uses the example of biofilms to examine Hull's (1980) and Godfrey-Smith's (2009) accounts of biological individuality and to explore the nature of individuality more generally. Biofilms are single or multispecies communities of microorganisms. Biofilms are useful for examining accounts of biological individuality because they fail to satisfy commonly suggested properties of biological individuals, such as having reproductive bottlenecks, forming parent-offspring lineages, and being composed of members of the same species. Nevertheless, biofilms have many of the other qualities associated with biological individuals. Biofilms are embedded in a self-produced extracellular substance that prevents predation, captures nutrients, and allows the cells of a biofilm to communicate and share genes. Biofilms have repeatable life cycles, and they have biofilm-level adaptations that vary among biofilms. On some accounts of reproduction, they are reproducers. Whether there is inheritance between earlier and later biofilms is an open question. Nevertheless, there is trait transmission between earlier and later biofilms, even though biofilms form via aggregation.

Biofilms provide a good case for studying biological individuality. The nature of biofilms, for example, suggests that Godfrey-Smith's account of biological individuality is too restrictive. Biofilms fare poorly on Godfrey-Smith's account of individuals because they fail to have reproductive bottlenecks, they do not stand in the appropriate parent-offspring relations, and their reproductive division of labor is not high. Despite violating Godfrey-Smith's criteria for paradigmatic or middling individuals, biofilms fulfill many (if not all) of his underlying desiderata for individuals in natural selection, which gives us reason to think they are in fact individuals.

In this chapter we support Hull's interactor account of individuality. We do so for two reasons. One is that according to Hull's account of individuality biofilms are good candidates for interactors in natural selection and hence individuals in natural selection. The other reason is that Hull's interactor account of biological individuality can be placed in a more general interactor account of individuality, one that extends beyond biology. In what follows we develop an interactor account of individuality in the tradition of Hull's, but we renovate Hull's theory in several ways. First, we place it in a general sortal framework, along the lines of Wiggins's (2001) sortal account of identity. There are different sorts of individuals in the world, and when asking if an entity is an individual we need to specify the sort of individual under consideration. Second, we dive into the metaphysics of individuality, articulating the different types of processes (internal interaction versus external forces) that cause entities to be parts of an individual. Third, we depart from Hull's commitment to replicator theory and allow for a more liberal account of reproducers. In the end, we offer an interactor account of biological individuality embedded in a more general theory of individuality.

6.2 Biofilms: A Primer

Let us start by introducing our case study. Biofilms are found throughout the environment. They grow on the rocks of rivers, on the surfaces of stagnant water, and on our teeth. The bacteria of a biofilm collectively produce, and are embedded in, an extracellular polymeric substance (EPS). EPS matrices hold the cells of a biofilm together. More interestingly, they are digestive systems that trap nutrients in the environment and break those nutrients down with extracellular enzymes (Flemming and Wingender 2010). EPS matrices also protect biofilms with molecules that bind to antimicrobial agents and prevent their access to biofilm cells. In addition, EPS matrices are media for cell communication among the bacteria of a biofilm, and they foster the exchange of genetic material through lateral gene transfer (see below).

The life of a biofilm proceeds through a series of stages (Hall-Stoodley, Costerton, and Stoodley 2004). For example, a multispecies oral biofilm begins its life cycle with first colonizers, *Streptococcus gordonii*, attaching to tooth surfaces. Then secondary colonizers from the species *Porphyromonas gingivalis* coaggregate with the cells already attached (Kolenbrander et al. 2010). Coaggregation is "a process by which genetically distinct bacteria become attached to one another via specific molecules" (Rickard et al. 2003, 94). It is common for biofilm formation to be a sequential process involving different species at different stages

(Kolenbrander et al. 2010). Once a biofilm is fully colonized it matures. Then, in its last stage, dispersal cells are produced and released to the environment. A biofilm life cycle, thus, consists of four stages: planktonic lifestyle (unattached single cells); attachment; colonization; and dispersal.

The cells of a biofilm interact in numerous ways. Quorum sensing, for example, is a cell-to-cell signaling system that enables bacteria within a biofilm to regulate cellular density. Quorum sensing occurs through the secretion and detection of molecules called "autoinducers." When the concentration of autoinducers reaches a certain threshold, cell differentiation in a biofilm is affected (Davies et al. 1998). Another signaling system, called "molecular signalling," affects a biofilm's lifecycle. For example, low concentrations of nitric oxide produced by *P. aeruginosa* trigger biofilm dispersion (Stewart and Franklin 2008).

Another type of biofilm interaction is lateral gene transfer (LGT). LGT is gene transfer among bacterial cells that is not due to reproduction. It occurs among conspecific strains and strains in different species. Biofilms provide favorable conditions for LGT. Consider two LGT mechanisms: transformation and conjugation. Transformation consists of the uptake of free DNA from the environment by a bacterial cell. Transformation requires extracellular DNA. In biofilms this prerequisite is met because environmental DNA is a major constituent of biofilms. The other mechanism for LGT, conjugation, occurs via cell-to-cell junctions or bridges. Such bridges allow the transfer of mobile genetic elements, usually plasmids. The physical stability caused by EPS matrices reduces the chance of conjugal bridges breaking (Ehrlich et al. 2010). In short, lateral gene transfer occurs within biofilms for several reasons: the occurrence of extracellular DNA, high cell density, and the physical stability EPS matrices provide.

Stepping back from these details, we see that biofilms have repeatable life cycles. Those cycles are caused by various types of interactions within biofilms, such as quorum sensing, molecular signaling, aggregation, and lateral gene transfer. In addition, EPS matrices serve as digestive systems, defense mechanisms, and media for communication. Biofilms are not mere agglomerations of organisms but groups of organisms with multiple finely tuned interactions. Though some biofilms contain only conspecifics, many biofilms are composed of organisms from multiple species.

6.3 Godfrey-Smith's Account of Biological Individuality

Godfrey-Smith's (2009, 2013) account of biological individuality starts with Lewontin's (1985) characterization of natural selection. According to Lewontin, natural selection occurs when three necessary conditions are met: there is variation among individuals; that variation is heritable; and that

variation results in differential fitness among individuals. Godfrey-Smith explores all three of Lewontin's conditions for selection, but he pays special attention to the role of reproduction in selection. As Godfrey-Smith (2009, 86) writes, "The link between 'individuality' and reproduction is … inevitable. Reproduction involves the creation of a new entity, and this will be a countable individual." Individuals in natural selection must be reproducers: those entities that not only vary and have differential fitness, but also have countable descendants.

Godfrey-Smith's discussion of reproducers focuses on what he calls "collective reproducers": "reproducing entities with parts that themselves have the capacity to reproduce, where the parts do so largely through their own resources rather than through the coordinated activity of the whole" (2009, 87).[1] Multicellular organisms are collective reproducers. Godfrey-Smith measures such reproduction using three parameters. Those parameters come in degrees. The higher an entity scores on the parameters, the closer it is to being a paradigmatic individual. The first parameter is reproductive bottleneck. According to Godfrey-Smith, paradigmatic cases of reproduction require a bottleneck, such as when a zygote develops from a small propagule. Human reproduction involves such bottlenecks. No bottleneck occurs when a new structure is formed by the aggregation of cells, for example when free living *Dictyostelium* cells aggregate and form a slime mold (2009, 95). Godfrey-Smith's second parameter measures the degree of reproductive division of labor within a reproducer. Humans score high because we have distinct germ and soma lineages, where the first type of lineage is responsible for reproduction. Sponges, on the other hand, score low on this parameter when they reproduce asexually because any fragment of a sponge can start a new sponge (2009, 92). Godfrey-Smith's third parameter, integration, concerns the boundary between an individual and its environment, and the mutual dependence of its parts. Mammals have high integration, buffalo herds have low integration, and sponges somewhere in between.

Are biofilms reproducers and individuals on Godfrey-Smith's account? Let's start with the bottleneck parameter. A bottleneck occurs when a new individual develops from a small propagule. A bottleneck does not occur when a new individual is the result of the aggregation of numerous cells. As we saw earlier, biofilms form by aggregation. Consequently, they lack bottlenecks. Though biofilms fail Godfrey-Smith's bottleneck criterion for reproduction, they nevertheless satisfy his reason for positing bottlenecks as a condition for paradigmatic individuality. Bottlenecks foster biological individuality because when a mutation occurs in the germ line of an organism, a bottleneck spreads that genetic change to an individual's somatic cells. As Godfrey-Smith writes, "Because a bottleneck forces the process of growth and development to begin anew, an initially localized mutation

can have a multitude of downstream effects" (2009, 91). Biofilms have an alternative process for doing this—lateral gene transfer. Biofilm evolution is due in no small part to the introduction of new genetic material in a biofilm, and then the transfer of that material to other parts of a biofilm. For example, Ehrlich and coauthors (2010) posit the Distributed Genome Hypothesis (DGH) to explain the abundance of biofilms that cause chronic disease by citing the role of LGT in biofilms. According to DGH, new disease strains are caused by novel combinations of genes that are spread throughout a biofilm by LGT. The example of DGH illustrates how LGT distributes genes in a collective that lacks a bottleneck. It illustrates how Godfrey-Smith's motivation for requiring bottlenecks for paradigmatic or marginal individuals can be satisfied when there is no bottleneck present.

While biofilms score poorly on Godfrey-Smith's bottleneck parameter, they have an intermediate score when it comes to division of reproductive labor. Recall that humans score high on this parameter: few of our parts are passed on, just our gametes. Sponges, when they reproduce asexually, score poorly on reproductive division of labor because any part can start a new sponge. Slime molds score in the middle: they have "some reproductive specialization," though more of their parts can reproduce than the parts of a mammal (Godfrey-Smith 2009, 95). Biofilms are in the same boat as slime molds when it comes to division of reproductive labor. More parts of a biofilm can start a new biofilm than the parts of a mammal can start a new mammal. Nevertheless, there are specialized reproductive cells in a biofilm, in contrast to the cells in a sponge. For example, a biofilm's planktonic cells are dispersal cells and the source of new biofilms, whereas sessile cells primarily perform the function of helping biofilms adhere to surfaces. Biofilms, thus, score somewhere near the middle on Godfrey-Smith's criterion of division of reproductive labor.

Biofilms do well on Godfrey-Smith's third parameter for reproduction, integration. Godfrey-Smith measures integration by how effectively an entity maintains its boundary between itself and the environment, and how much its parts depend on each other for their viability. Biofilms are distinct from their environments. The cells of a biofilm are molecularly bonded through aggregation and bounded within an EPS matrix. An EPS matrix catches and digests nutrients from the environment and protects a biofilm's cells from predators. Furthermore, the cells of a biofilm share genetic material via LGT, and there is intercellular communication within a biofilm that regulates a biofilm's development. These interactions set a boundary between a biofilm and its environment (more on this below). Biofilms also score high on Godfrey-Smith's other measure of integration, the degree to which the parts of an individual rely on each other for their viability. There are a number of biofilm-level processes that cause bacteria to have a significantly higher survivorship when they are part of a biofilm

than when they live on their own (Costerton 2007). For example, a biofilm's EPS matrix contains chemicals that protect its component bacteria, and it contains mechanisms for catching and digesting nutrients.

Stepping back from these details, we see that biofilms lack bottlenecks, they score somewhere in the middle when it comes to division of reproductive labor, and they score high on integration. For Godfrey-Smith, paradigmatic reproducers, and consequently paradigmatic individuals, need to score high on all three parameters (2009, 94). Biofilms do not—they fail to have bottlenecks and are middling on division of reproductive labor. Nevertheless they score high on integration because they have a number of processes that promote their stability and demarcate them from the environment. Moreover, though biofilms fail to have bottlenecks, they satisfy Godfrey-Smith's motivation for requiring that paradigm individuals have bottlenecks: to spread mutations among the parts of an individual. Biofilms do this through LGT. Biofilms satisfy this desideratum of Godfrey-Smith's account, yet they fail to satisfy his specific criteria for being either paradigmatic or middling individuals. This gives us reason to think that biofilms are individuals in natural selection, and that Godfrey-Smith's account, as it stands, is too restrictive an account of individuality.

Biofilms reveal a further problem with Godfrey-Smith's account, namely his view of what sort of parent-offspring lineages can form individuals. Some biofilms are multispecies. Godfrey-Smith allows the existence of multispecies individuals so long as the different species lineages within an individual run in tandem (2013). He cites the case of aphids and their symbiotic bacteria to demonstrate this. These bacteria and their host aphids have the same reproductive cycle: an aphid mother transfers bacteria to its offspring through its ovary. Biofilms, however, do not consist of lineages that run in tandem. The bacteria that form a biofilm are scattered in the environment and they come from different sources. Furthermore, their coaggregation occurs at different stages of biofilm formation. In other words, the different bacterial lineages that comprise a biofilm do not run in tandem, and they fail to form a unified parent-offspring lineage in Godfrey-Smith's sense. More generally, biofilms serve as a counterexample to the requirement that an individual be composed of lineages that have the same beginnings and endings. We hasten to add that the occurrence of LGT in biofilms and not in aphid-symbiont combinations (Nikoh et al. 2010) makes biofilms better candidates for biological individuals than aphid-symbiont combinations.

Before leaving Godfrey-Smith's account of individuality, we should address several possible objections to biofilms being biological individuals. First, one might worry that biofilms are ecological communities and not individuals. We have tried to address that concern above. To emphasize that biofilms are individuals and not merely communities, contrast biofilms

with common examples of symbiotic complexes, such as the symbiotic relation between ants and acacias (Godfrey-Smith 2011). Bacteria in a biofilm exchange genetic content; ant/acacia symbionts do not. Bacteria within a biofilm build and employ EPS matrices. Such matrices, as we have seen, defend a biofilm's bacteria from predators, capture and digest nutrients, and facilitate communication among component bacteria. The sorts of interactions and interpenetrations that occur among the bacteria of a biofilm outstrip symbiotic and other kinds of ecological relations.

One might grant that biofilms are more organized than ecological units, but nevertheless maintain that biofilms are not individuals in natural selection, that they are something in between. For example, Godfrey-Smith (2013) discusses metabolic organisms. A metabolic organism is a system of entities that collectively work together using environmental resources to maintain that system. For Godfrey-Smith, some organisms fail to be individuals (in natural selection) because they do not form reproductive lineages. Godfrey-Smith explains his individual/organism distinction using the example of squid-bacteria symbiotic complexes. Godfrey-Smith argues that such complexes are not individuals in natural selection because each complex is "a metabolic knotting of reproductive lineages that remain distinct" (2009, 30). Using this concept of organism, one might object that biofilms are not individuals (in natural selection) but merely organisms as Godfrey-Smith defines them. We respond by pointing out that biofilms are not simply organisms *sensu* Godfrey-Smith. Bacterial lineages within a biofilm do not remain distinct, as do the lineages of squids and their symbiotic bacteria. Lateral gene transfer genetically blends the different species lineages of a biofilm. Then there are the other interactive processes among the bacteria of a biofilm that we have discussed, such as the production of a common EPS matrix that protects biofilms from predators, captures and digests nutrients, and allows cells to communicate for biofilm growth. The interactions and interpenetrations among the bacteria of a biofilm outstrip the interactions among the members of symbiotic consortia. A biofilm is more than a mere metabolic knotting of bacteria.

Finally, one might worry that if biofilms are not reproducers given Godfrey-Smith's multifaceted account of reproduction, then biofilms are not reproducers at all. And if biofilms are not reproducers, then they are not individuals in natural selection. We address this concern in section 6.5.

6.4 An Interactor Account of Individuality

In this section we turn to an interactor account of individuality. Our aim in this section is threefold. First, we offer a general interactor framework for individuality—general in the sense that it applies to biological

and nonbiological individuals. Second, we discuss Hull's (1980) interactor account of individuality and demonstrate that biofilms are individuals under that account. Third, we discuss how biofilm biology raises the question of what sort of interaction is required among the parts of an individual.

The general interactor framework we suggest has two components. First there is a sortal component: when asking if X is an individual we need to ask if X is an individual of sort S. Here we follow Wiggins's (2001) sortal account of identity. When asking if two entities are the same entity, we need to place that entity under a sortal and enquire about the identity conditions for the sort of entity in question. The guiding idea is that different sorts of entities have different identity conditions. We follow a similar route when it comes to individuals. When asking whether something is an individual we need to specify the sort of individual under consideration. Evidence for this sortal approach to individuality is found in the different sorts of individuals in biology and their varying identity conditions. There are individuals in natural selection (the focus of this chapter), individuals in systematics (species and other taxa, Hull 1978), metabolic individuals (Godfrey-Smith 2013), immunological individuals (Pradeu 2010), and perhaps other types of biological individuals.

The second component of this interactor framework concerns the interactions necessary for an entity to be a certain sort of individual. Individuals of different sorts have different outcomes (functions, states, products). Consider two examples: individuals in natural selection require processes that allow them to vary and pass on that variance; individuals in biological systematics require processes that cause them to be distinct lineages. Once we determine the sort of individual under investigation and the outcomes necessary to be that sort of individual, our focus turns to the types of interactions required of individuals of that sort. We need to ask if the parts of an entity appropriately interact among themselves or with the environment to form the sort of individual in question. This framework for individuality is quite general. It applies to various kinds of individuals, both in and outside of biology.

How this framework applies to individuals in biology will be demonstrated shortly. But first let us briefly mention how it applies to individuals outside of biology. Armstrong (1980) provides a causal theory of individuality that is an interactionist account. He uses the example of individuating a cup to illustrate his account. Suppose the function of cup is to be a solid material that holds liquid. In order for cup parts to form an individual that holds liquid, those parts must be appropriately attached. According to Coulomb's law, objects are bound into a solid that can hold water only if there are certain electrostatic forces among the molecules in those objects (Halliday, Resnick, and Walker 2013). Consequently, cup parts are parts

of an individual cup only if there are certain electrostatic forces among molecules in those parts. This is a simple example and offered merely to indicate that an interaction account of individuality is applicable beyond biology.

Returning to biology, numerous philosophers adopt an interactor account of individuals in natural selection (for example, Hull 1980, Sober and Wilson 1998, Lloyd and Gould 1993, Dupré and O'Malley 2009). Here we will discuss Hull's (1980) interactor account of individuality, which is embedded in his interactor-replicator framework for natural selection. In that framework, interactors and replicators are both necessary for natural selection. According to Hull, replicators "pass on their structure largely intact from generation to generation" (1980, 315). Genes and asexual organisms are replicators for Hull. Though some asexual parents and offspring may not be genetically identical, they are similar enough to pass Hull's standard. Sexual organisms, colonies, and more inclusive units are not replicators. Recombination in sexual reproduction, for instance, reshuffles the genetic contributions of parents so that sexual offspring fail Hull's criterion for replicators. Turning to interactors, an interactor is "an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential" (1980, 318). Hull suggests that organisms and perhaps colonies are interactors, but he is suspicious of more inclusive entities being interactors (1980, 325). In Hull's theory of natural selection, both replicators and interactors must be present for selection to occur, but they need not be the same entities. In fact, very few entities are both replicators and interactors. Hull suggests that genes fulfill both roles (1980, 320). In the majority of cases, interactors and replicators occur at different hierarchical levels, for example, some organisms are interactors and their genes are replicators.

Are biofilms replicators or interactors on Hull's account? Let us start with replicators. According to Hull (1980, 315) replicators must pass on their structure "largely intact." Hull tells us that the entire genome of an asexual organism is a replicator because "in asexual reproduction, the entire genome is transmitted" (1980, 321). In contrast, the genomes in sexual organisms may be altered by recombination, so only portions of the genomes in sexual organisms are replicators. Just as not all of the genes of a sexual parent make it into an offspring, not all of the strains of a biofilm make it into a descendent biofilm (Kolenbrander et al. 2010, 478). Furthermore, according to Ehrlich and coauthors (2010, 270), lateral gene transfer "among the component strains (and species) [of a biofilm] leads to the continuous generation of a cloud of new strains with a novel combination of genes." In other words, LGT can cause a biofilm to genetically change over time. Biofilms vary too much to be replicators. Nevertheless, biofilms contain replicators, their genes and bacterial cells.

Are biofilms interactors on Hull's account? Hull places two restrictions on interactors. First, an interactor must be a cohesive whole. Second, an interactor's interaction with the environment must have a unitary effect on its constituent replicators. Starting with the notion of cohesive whole, Hull contrasts such wholes with mere groups. Mere groups are spatio-temporally localized, but that is merely due to their being at the same location (Hull 1980, 314). Interactors should be more because "[a mere] group can be selected only incidentally—e.g., because all its members happen to be in close proximity to each other" (314). Hull also describes interactors as "functionally organized systems" and "organized wholes" (325). He adds that populations are interactors only if they have "populational adaptations, properties characteristic of the population as a whole that allow it to interact with the environment as a whole" (325). Biofilms satisfy the cohesive whole requirement for being an interactor. Biofilms are not mere groups of organisms that happen to be at the same location at the same time. *P. gingivalis*, for example, does not become part of an oral biofilm simply because it happens to be near other colonizers. *P. gingivalis* becomes part of a biofilm through coaggregation (Hojo et al. 2009), and coaggregation mechanisms restrict which species can bind together (Rickard et al. 2003). Then there are mutualistic interactions among the species of a biofilm in which the byproduct of one species' metabolism is utilized by another species within that biofilm (Stewart and Franklin 2008). In general, the orchestra of cell-to-cell interactions within a biofilm shows that biofilms are not mere groups but cohesive wholes *sensu* Hull.

What about Hull's second condition for being an interactor, namely that an interactor's interaction with the environment has a "unitary effect" on its constituent replicators? Does a biofilm's interaction with the environment have a unitary effect on its constituent replicators? If "unitary effect" means that the failure or success of a biofilm affects the survivorship of its constituent cells (replicators) in a uniform way, then biofilms meet this condition. Bacterial cells typically have higher survivorship when they are parts of a biofilm than when they are in their planktonic state (Costerton 2007). There are multiple reasons. EPS matrices help protect bacteria from antimicrobial agents (Flemming and Wingender 2010). Biofilms allow bacteria to withstand shear stresses in flowing environments (Hall-Stoodley, Costerton, and Stoodley 2004, 99). And by forming biofilms, bacterial cells form "opportunistic self-mobilizing communities" capable of surviving environments, such as the deep ocean, that bacteria by themselves could not survive (Costerton 2007, 64ff.). The capacity to form biofilms is central for explaining the proclivity of bacterial cells. A biofilm's interaction with the environment *as a biofilm* has an important unitary effect on its bacterial cells: it increases their survivability.

One might worry that biofilms are no more interactors whose interactions have a unitary effect on their constituents than symbiotic consortia or ecological groups. We agree that symbiotic consortia and ecological groups have interactions that affect their constituents. In the squid-bacteria consortium discussed earlier, a selection force against the bacteria will negatively affect the squid that depend on those bacteria for camouflage. Similarly, selection that affects a segment of a buffalo herd and reduces the available gene pool for the herd may decrease the fitness of all. Generally, the number of interactions a group experiences and the extent to which those interactions affect all the members of a group come in degrees. We contend that the interactions among the members of a biofilm and the degree to which they affect its members surpass the interactions among the members of an ecological group. As discussed throughout this chapter, the bacteria of a biofilm have a robust number of interactions: from EPS formation to quorum sensing, from shared defensive and nutrient-gathering mechanisms to the sharing of genetic material. The interactions and interpenetrations are more numerous than symbiotic interactions. Moreover, the sharing of genes through LGT demonstrates that the interaction among a biofilm's members has a more significant genetic downstream effect than found in symbiotic consortia or ecological groups. The interactive effects among the constituent replicators of a biofilm are more uniform than similar effects among the replicators of an ecological group.

The upshot is that biofilms are good candidates for interactors and consequently individuals on Hull's natural selection account of individuality. On Hull's account, biofilms are individuals in natural selection, despite their lacking reproductive bottlenecks, despite their being multispecies individuals, and despite their not forming single parent-offspring lineages. Given this result and a result of the previous section (that biofilms satisfy many of Godfrey-Smith's underlying desiderata for individuality), we believe that biofilms are good candidates for individuals in natural selection. We also offer further reasons for thinking that biofilms are individuals in natural selection in the next section. Given how well Hull's account of individuality captures biofilms as individuals in natural selection, we prefer his account to Godfrey-Smith's.

Before leaving this section we would like to discuss the metaphysics of the cohesiveness or interaction required of the parts of an individual. The nature of biofilms suggests that such interaction is less intuitive than one might think. Recall Armstrong's example of the sort of interaction required among the parts of a cup for it to be parts of a cup: electrostatic interaction among the different parts. That sort of interaction is internal to the individual in question. We would like to suggest that the sort of interaction required among the parts of individual could be due to external forces acting on those parts. When Hull tells us that an individual in

natural selection needs to be a cohesive whole whose interaction with the environment has a unitary effect on its replicators, does he require that the parts of the individual causally interact with each other, or can acting in a unity fashion due to environmental forces suffice for being an individual?

Hull does not address this question in his work on selection, but he does in his work on species. He writes that the sort of cohesion needed for a species to be an individual lies in its organisms having "fairly consistent, recognizable phenotypes" (1978, 343). He also tells us that such cohesion can be the result of processes that require the members of species to causally interact, or the result of processes that act independently on those organisms (1978, 343–344). Gene flow among the members of a species is an example of an interactive process among the members of a species. Genetic homeostasis and exposure to common selection regimes are examples of cohesifying mechanisms that act independently within or on members of a species. Genetic homeostasis is internal to each developing organism. Exposure to common selection regimes is the effect of the environment on each organism. So for Hull, external forces acting on organisms, not just interactions among a species' organisms, contribute to the cohesiveness of an individual.

What about interactor individuals in natural selection? Can they be individuals due to external processes acting on the parts of an individual rather than interactive processes among those parts? We will not provide a definitive answer to this question, but suggest that just like the parts of a species, the parts of an interactor in selection may be parts of that interactor due to external forces. As an example, consider cooperation among the parts of a biofilm. The literature on cooperation among the cells of a biofilm centers on the notion of public goods. Public goods are costly products manufactured by some cells that benefit other cells in a biofilm, such as signaling molecules (for quorum sensing) and EPS compounds. The existence of public goods in biofilms poses the problem of what prevents the spread of cheats within a biofilm—those cells that benefit from the products of other cells but do not themselves produce public goods. There are several suggested mechanisms that foster cooperation among the cells of a biofilm. We discuss one.

One set of experiments focuses on the bacterial species *Pseudomonas fluorescens* (Brockhurst, Buckling, and Gardner 2007). A strain of *P. fluorescens*, the wrinkly spreaders, produces a public good, cellulosic polymer, which improves access to oxygen by enabling the construction of biofilms at the surface of liquids. However, biofilms with the wrinkly spreader strain are susceptible to invasion by another strain of *P. fluorescens*, the smooth spreaders: they reap the benefits of being part of a biofilm without paying the cost of building the biofilm. Brockhurst, Buckling, and Gardner (2007) show that some forms of ecological disturbance promote biofilms

with cooperating cells. In their work, they varied the degree of ecological disturbance affecting the biofilms under study. Brockhurst, Buckling, and Gardner (2007) found that under frequent disturbance, the density of cells is below the level at which biofilm formation is beneficial. Under intermediate ecological disturbance, the proportion of cooperators (wrinkly spreaders) peaks. When there is infrequent disturbance, the number of cheaters increases significantly and biofilms produce fewer public goods. Thus, in cases of intermediate ecological disturbance, selection favors biofilms with higher proportions of cooperators. Brockhurst, Buckling, and Gardner's (2007) work shows that ecological disturbance can be an external force that keeps cheaters in check.

The metaphysical implication of this finding is that a group of organisms can, at least in part, be caused to be an interactor due to external forces acting on those organisms. Biofilms of *P. fluorescens* vary in their proportions of cheats and noncheats. Those with higher proportions of noncheats pass on more cells that form biofilms than biofilms with lower proportions of noncheats. That variation in proportions of cheats and noncheats among biofilms is at least in part caused by environmental causes. According to Hull, an interactor's interaction with the environment should have a unitary effect on its replicators, and among interactors that replication should be differential. That is happening among *P. fluorescens* biofilms due to external forces acting on the cells of those biofilms. This is an interesting metaphysical result. This biofilm example and Hull's species example raise the question of whether the sort of interaction required for individuality must be internal to an individual or if it can be due to external forces acting on that individual. At the very least, these examples show that one type of interaction that contributes to the individuality of some individuals is the environment acting on the parts of those individuals.

6.5 Reproducers, Inheritance, and Natural Selection

A concern raised in section 6.3 is that if biofilms are individuals in natural selection, then they need to be reproducers.[2] Recall that biofilms score poorly on Godfrey-Smith's (2009) parameters for reproducers. Biofilms lack bottlenecks, even though they perform the desideratum for bottlenecks—the spreading of genetic novelty within an individual. Biofilms are at best middling on his criterion of division of reproductive labor. And biofilms do not form the sort of parent-offspring lineages Godfrey-Smith attributes to individuals. We could at this stage say that we do not care if biofilms are reproducers and point out that in Hull's (1980) interactor-replicator framework it does not matter whether biofilms are reproducers. Biofilms

just need to be interactors with appropriately related replicators, and in the previous section we suggested that biofilms are such interactors.

Nevertheless, we think a case can be made for biofilms being reproducers using Griesemer's (2000a, 2000b) account of reproduction. According to Griesemer, reproduction is the "multiplication with material overlap of mechanisms conferring the capacity to develop" (2000a, 361). There are two parts to this account. First, parents and offspring must have a genealogical relationship caused by material overlap. Second, entities capable of reproducing must develop or have life cycles. Griesemer describes development as the acquisition of the capacity to reproduce (2000a, 360). For Griesemer, "The realization of a reproduction process entails the realization of a developmental process. The realization of development entails reproduction" (2000b, 74). This interdependence between reproduction and development forms a hierarchical structure. The reproduction of a multicellular organism requires an organism to develop from cells; cell reproduction requires cells to develop from organelles and chromosomes; and so on. This hierarchy bottoms out at the level of "null development," which is a case of reproduction of offspring that lack the capacity to develop (Griesemer 2000a, 362).

Biofilms satisfy Griesemer's account of reproduction. Once a biofilm matures, it releases cells to the environment, either as individual cells or as clumps of cells. For example, *P. aeruginosa* biofilms produce motile cells that swim out of a biofilm, and *S. aureus* biofilms shed clumps of hundreds of nonmotile cells (Hall-Stoodley, Costerton, and Stoodley 2004). The released cells, or their descendants,[3] aggregate with other cells and form new biofilms. New biofilms, thus, are built using material contributed by old biofilms. Furthermore, that material provides new biofilms with the capacity to develop. As we saw in section 6.2, biofilms have four developmental stages in their life cycles: planktonic lifestyle, attachment, colonization, and dispersal. Biofilm development also has the reproduction-developmental hierarchy that Griesemer proposes. The reproduction of a biofilm requires a biofilm to develop from cells; and cell reproduction requires cells to develop from organelles and chromosomes.

Biofilms reproduce according to Griesemer's account. Furthermore, we have seen that biofilms are interactors with appropriately related replicators. Still, one might be committed to Lewontin's (1985) framework for natural selection and wonder if biofilms satisfy his requirements for individuality. Recall that according to Lewontin, entities are individuals in natural selection if three conditions are met: there is variation among individuals; that variation is heritable; and that variation results in differential fitness among individuals. Similarly for Griesemer, being a reproducer is not sufficient for being an individual in natural selection. Griesemer writes that more is needed. "So long as the components of development

by which the capacity to reproduce is acquired result in component transmission fidelities greater than zero there is scope for evolution to operate among them. Populations of reproducers have the capacity to evolve, insofar as the pieces of development that realize their reproductive capacities themselves have heritable properties that vary" (Griesemer 2000a, 363). For the remainder of this section we explore the question of whether there is heritable, adaptive variation among biofilms.

Biofilms reproduce by aggregation, and at first glance that seems to undermine their having heritable variation. The cells that aggregate to form a biofilm often come from different biofilms, and they often come from different species. In addition, the particular species compositions of earlier and later biofilms can vary (Kolenbrander et al. 2010). For example, oral biofilms usually contain the species *S. mutans*, but such biofilms can be formed without that species. It seems that the transmission of genetic information, or any information, among earlier and later biofilms is too diffuse, too disorganized for there to be heritable variation among biofilms. However, we think that this conclusion is too hasty given current empirical work on biofilms. Consider oral biofilms that usually contain the species *S. mutans*. That species can be absent in a new oral biofilm, yet that biofilm still forms and is "caries inducing" without *S. mutans* (Kolenbrander et al. 2010, 478). In other words, the biofilm phenotype "caries inducing" occurs even when there is variation in the species composition of an oral biofilm. There is a general point here. Oral biofilms and other biofilms reliably exhibit a number of adaptive traits across biofilm generations, such as quorum sensing, EPS production, mutualist interactions, and other life cycle traits (see section 6.2). That seems uncontroversial. The pressing question is, how do these traits get reliability transmitted through aggregation? Or to put it differently, if biofilms reproduce via aggregation, how do they have "transmission fidelities greater than zero" (Griesemer 2000a, 363)? Empirical work on this question is in its early stages, but there seem to be at least two mechanisms that cause such transmission.

First, recall that not all species can aggregate with each other to form a biofilm. Bacteria do not form a biofilm because they happen to be near each other. There are specific molecular mechanisms that determine which bacteria can aggregate with each other. For instance, *F. nucleatum* acts as bridge between early and late colonizers in the formation of oral biofilms (Hojo et al. 2009). Mechanisms that regulate how biofilms form by aggregation also regulate which cells and genes get transmitted between older and newer biofilms. Another transmission mechanism in biofilms is lateral gene transfer (LGT). We have discussed how LGT transfers mutations within a biofilm. LGT also transfers genetic material among biofilms and is a mechanism for biofilm inheritance. Consider work on the mechanisms that foster cooperation among the bacteria in a biofilm. One set

of experiments focuses on mobile genetic elements (MGEs)—genes that can move among prokaryotic genomes via LGT. MGEs are akin to infectious agents, capable of benefiting or harming their bacterial hosts. Smith (2001) hypothesizes that if cooperation is coded in MGEs, then the lateral transfer of these mobile elements may infect noncooperative bacteria, causing them to become cooperative and produce a public good. Nogueira and coauthors (2009) provide empirical evidence for Smith's hypothesis by studying the genes that code for the protein secretome. Such proteins are costly to produce, yet they benefit neighboring bacteria. Nogueira and coauthors (2009) found that the genes coding for secretome are overrepresented in MGEs and are laterally transferred among and within biofilms. LGT in this case keeps the number of cheats in check. This example illustrates how transmission of a trait can occur among biofilms even though biofilms reproduce by aggregation. It is also an example of a transmitted trait that increases the fitness of a biofilm: biofilms with fewer cheaters do better than biofilms with more cheaters (see section 6.4 and Brockhurst, Buckling, and Gardner 2007).

Stepping back from these details, we believe that biofilms may indeed satisfy Lewontin's three criteria for individuals in natural selection. Work on biofilms indicates that they do have mechanisms for nonzero transmission fidelity. Furthermore, the suggestion that biofilms are connected by inheritance seems plausible given that biofilms have traits that affect the fitness of whole biofilms and their component bacteria, and those traits occur over and over again. When it comes to the general question of whether biofilms are reproducers with the sort of inheritance needed to be individuals in natural selection, we can say the following. Biofilms are individuals in Hull's framework because they are interactors with appropriately related replicators. There is promising evidence that biofilms may be individuals in natural selection according to Lewontin's and Griesemer's frameworks. However, biofilms are poor individuals according to Godfrey-Smith's account.

6.6 Conclusion

In this chapter we have offered an interactor account of biological individuality embedded in a more general theory of individuality. That general approach to individuality employs a sortal framework: the world consists of different sorts of individuals, and whether or not an entity is an individual depends on whether that entity's parts interact (among themselves or with its environment) in a sortal-specific way. We see the inclusiveness of this framework as a virtue—it allows for multiple theories of individuality corresponding to the multiple kinds of individuals in the world.

When it comes to biofilms, we have seen that their nature teaches us several things about individuality. First, it teaches us that some standard ideas about individuals in natural selection should be abandoned. Individuals in natural selection need not have bottlenecks or a high division of reproductive labor. Such individuals can be composed of lineages from different species, and those lineages need not run in tandem. Second, biofilms teach us that a proper theory of reproduction should be more inclusive than commonly conceived. Aggregation is not normally seen as reproduction, but through aggregation biofilms may pass on heritable variation. Third, biofilms teach us that common intuitions about the type of relations required among the parts of an individual may be wrong. Perhaps some individuals owe their individuality to external rather than internal processes. The lowly biofilm does teach us a thing or two about the metaphysics of individuality.

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Notes

1. Godfrey-Smith (2009) also discusses two other types of reproduction: simple and scaffolded. A simple reproducer reproduces using its internal machinery, but the parts of a simple reproducer cannot reproduce using their internal machinery. Scaffolded reproducers are reproduced by mechanisms external to them. Godfrey-Smith's discussion of reproduction focuses on collective reproduction, which we simply call "reproduction."

2. Bouchard (2010), however, questions this assumption. He suggests that in some cases we should count the fitness of an individual in terms of differential growth rather than differential reproduction.

3. Some bacterial cells multiply through binary fission during their planktonic stage.

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