

Biological Individuality Is Not Necessarily an Intrinsic Property

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A significant and longstanding debate in philosophy of biology has centered around biological individuality. Although there have been numerous attempts to articulate a plausible and unifying view of what makes something a biological individual, the results are often conflicting and non-coextensive. In spite of these disputes, an open consensus around a few general ideas has surfaced (Pradeu 2016a). One common assumption that has been carried over with the consensus is that biological individuality is an intrinsic property of biological entities (Clarke 2016a). This tendency is reflected in the properties typically selected as criteria: what makes something an individual is quite often a property that biological entities themselves possess. I draw on Ellen Clarke's (2013) evolutionary account of biological individuality, research about the evolution and maintenance of cooperation in the origins of multicellularity (Brockhurst et al. 2007; Gulli et al. 2019), and important parts of the consensus around biological individuality to argue against this trend. What makes something a biological individual is not always something about the entities in question. I show that there are environmental mechanisms capable of acting as individuation mechanisms in circumstances that resemble early transition stages, or in situations where individuality departs from paradigm cases. Therefore, biological individuality is not necessarily an intrinsic property.

Keywords

biological individuality • evolutionary individuality • natural selection • intrinsic properties • extrinsic properties • ecological disturbance • biofilms • snowflake yeast

1 Introduction

The idea that the world is inhabited by biological individuals is quite familiar. What exactly makes something a biological individual, however, is actually rather puzzling. A significant and longstanding debate in philosophy of biology has centered around this issue. There have been

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numerous attempts to articulate a plausible and unifying view of what makes something a biological individual in the natural world (Hull 1980; Wilson 2005; Godfrey-Smith 2009; Pradeu 2012; Clarke 2013). Although there is now a range of varying accounts of biological individuality, they often provide conflicting and non-coextensive results (Clarke 2010; Pradeu 2016a). Such results can be quite surprising, especially considering that a broad consensus around certain features of individuality has been reached (Pradeu 2016a). The consensus includes the idea that individuality is a matter of degrees, and that both the major transitions of evolution (Buss 1987; Maynard Smith and Szathmary 1995) and the levels of selection debates (Okasha 2006) have something to say about it.

One common assumption about the nature of biological individuality has boarded the consensus inadvertently. The assumption is that the individuality of biological entities is grounded on properties that these entities themselves possess (Clarke 2013). To put it another way, biological individuality is an intrinsic property (Clarke 2016a). An examination of biological individuality accounts defended in the past two hundred years (i.e., Lidgard and Nyhart 2017, 23) shows that the properties commonly selected as individuating criteria are often intrinsic to the entities in question. What these accounts maintain is that there is something *about* biological entities that makes them individuals.

This general view about the nature of biological individuality is not just one among others. It shapes how we think about biological individuals. It tells us where to look and what to ignore. If biological individuality is an intrinsic matter, grounded on properties and mechanisms confined to the boundaries of living beings, then it may be reasonable to ignore or remove some biological entities from our consideration, especially if they lack suitable intrinsic properties. Committing to this overarching perspective would not be an issue if it was appropriately justified either by what is known about the evolutionary processes that originated most of the uncontroversial biological individuals, or by the frameworks commonly employed to deal with biological individuality. The problem, I contend, is that neither justify the intrinsic stance.

In this paper I argue that biological individuality is not necessarily an intrinsic property. I draw on a Darwinian framework that has been developed in the past forty years (Hull 1980; Godfrey-Smith 2009; Clarke 2013) and assume most of the received consensus around biological individuals (Pradeu 2016a). The arguments against the intrinsic stance build on Clarke's (2013) functional account of evolutionary individuality and follow a suggestion: in some borderline scenarios, environmental factors might be responsible for biological individuality (Clarke 2013; Ereshefsky and Pedroso 2015b). I will consider two examples unified by certain features. Both involve marginal selective processes and biological entities that resemble those found at early stages of evolutionary transitions. The examples suggest that in marginal transition events there are environmental factors capable of acting as individuation mechanisms.

The paper is structured in the following manner. The second section introduces part of the toolkit of the paper, including distinctions between intrinsic and extrinsic properties, and others between scaffolded and external mechanisms. The third section presents Clarke's (2013) account of biological individuality in detail. Once its functional features are in plain sight, I contrast her suggestion about the possibility of external individuating mechanisms with a subsequent commitment to biological individuality being an intrinsic property (2016a). In section 4 I explore Clarke's (2013) suggestion and develop two examples that might support it: biofilms and snowflake yeast cluster aggregates. Following Ereshefsky and Pedroso (2015b), I show that in the first case there are external mechanisms performing the roles that Clarke (2013) had conjectured. The second case exhibits a similar outcome: there are actual and possible external mechanisms capable of realizing functions normally attributed to intrinsic individuation properties. Finally, sections 5 and 6 address two objections. Section 5 questions the purported support

these cases provide for the main argument, namely, that biological individuality is not necessarily an intrinsic affair. The objection in section 6 puts in doubt the alleged individuality of the examples.

2 From Intrinsic and Extrinsic Properties to Scaffolded and External Mechanisms

Intrinsic and extrinsic properties can be characterized in various ways (Dunn 1990; Humberstone 1996; Francescotti 1999; Marshall 2016). However, most of the available accounts share a point of departure. The go-to analysis of the distinction is usually Lewis's (1983). According to Lewis, intrinsic properties are such that an object has them "in virtue of the way that thing itself, and nothing else, is" (197). By contrast, having an extrinsic property "may depend, wholly or partly, on something else" (197). These are properties that an object has "partly by virtue of how it relates to external items" (Francescotti 1999, 590). From an epistemological standpoint, "an intrinsic property would be a property that one could determine by inspection of the object itself" (Dunn 1990, 178). If we are dealing with physical objects, this means that we "would not have to look outside of its region of space-time" (178). The analysis of this rather intuitive distinction is typically spelt out by way of examples. In particular, examples that involve duplicates. "If something has an intrinsic property", claimed Lewis, "then so does any perfect duplicate of that thing." But the same is not true of extrinsic properties. The idea is that "duplicates situated in different surroundings will differ in their extrinsic properties" (Lewis 1983, 197).

The distinction between intrinsic and extrinsic properties is now a standard device in philosophers' toolkits and has been applied to a range of heterogeneous issues. G. E. Moore (1922), for example, used it as a basis for a further distinction, between intrinsic and extrinsic values. Intrinsic and extrinsic properties have also been put to work in attempts to account for the differences that underlie real and mere Cambridge change (Geach 1969; Humberstone 1996). Similarly, certain arguments for psychophysical supervenience, the idea that psychological traits and dispositions supervene on physical features, have relied on this distinction (Kim 1982). Further, Godfrey-Smith (2009) has made use of the intrinsic character of certain biological features to distinguish paradigmatic from marginal Darwinian populations. Finally, intrinsic and extrinsic properties have shown to be of some use in disputes between internalist and externalist views about cognition (Wilson 2014).

I intend to employ this distinction for one particular purpose. I believe that attention to the differences between intrinsic and extrinsic properties can foreground effective, but sometimes overlooked sources of biological individuality. In particular, sources that can be found outside the boundaries of biological individuals. The general strategy goes as follows. I assume that biological individuality can be treated as a multiply realizable, functional property (Clarke 2013). Among other things, this means that biological individuality can be realized by many different concrete properties, factors, or mechanisms. Put another way, it means that biological individuality might have different supervenience bases or realizers. The intrinsic stance, as I understand it, assumes that biological individuality supervenes solely on the intrinsic properties of biological entities. Thus conceived, biological entities are individuals purely in virtue of the intrinsic properties they have. These include mechanisms and traits of various kinds that remain even when external conditions change. By contrast, I argue that in some scenarios, the supervenience base of biological individuality is not restricted to the intrinsic properties that biological entities have. Sometimes, the supervenience base of biological individuality includes contingent environmental factors.

Intrinsic and extrinsic properties are key pieces of the conceptual toolkit, but they are not the only ones. Many of the details of the examples and arguments I develop throughout the paper rest on a further distinction between scaffolded mechanisms and external mechanisms. In various ways, this distinction mirrors some of the differences between intrinsic and extrinsic properties. I will start with a description of scaffolds in biology and relate all these distinctions afterward.

Usually, biological scaffolds are thought of as structures, mechanisms, or resources that support various processes. Among these, one can count development, reproduction, and a motley arrangement of cognitive endeavors (Caporael et al. 2014; Minelli 2016). In purely developmental domains, “scaffolds can be artifacts, infrastructure or other (biological, cognitive or cultural) agents that temporarily facilitate development of the system” (Griesemer 2014, 30). An issue with this rather broad initial approach is that multiple things could count as scaffolds, including food and other resources involved, for example, in metabolism. What distinguishes scaffolds from other environmental resources is that they neither “contribute material parts to the developing system” (Griesemer 2014, 30), nor are incorporated by it (Minelli 2016, 170). Thus, scaffolds stand as external aids, as “facilitating or catalyzing [parts] of the system’s environment” (Griesemer 2014, 30).

The examples I introduce in section 4 involve a series of mechanisms and environmental factors whose functions contribute to the individuality of biological entities. Each of them, however, does so in different ways. As I will suggest, some of the environmental factors in the examples act as scaffolds. In this setting, I regard scaffolds as external factors that support the development or function of properties and mechanisms that a biological entity already possesses. A mechanism of a biological entity that relies on an external factor for its development or functioning is a scaffolded mechanism. To advance my interpretation of the examples, and to defend some of them, I stress the differences between the scaffolds and scaffolded mechanisms I have just described and external mechanisms whose functions are decisive for the individuality of biological entities. In the context of the examples, a scaffolded mechanism is one whose contribution to individuality relies on the support of external factors, which are its scaffolds. Not all of the mechanisms that contribute to the individuality of biological entities are scaffolded, however. And not all of the external factors involved are mere scaffolds either. There are external mechanisms or factors in the examples that do not uphold the development or function of a scaffolded mechanism. Instead, these factors either supplant the function of a mechanism that a biological entity already possesses or exert a necessary function from the standpoint of individuality that would otherwise be absent.

This distinction between scaffolded mechanisms and external mechanisms can be linked to intrinsic and extrinsic properties in the following way. A scaffolded mechanism is an intrinsic property. Although its function is supported by external factors, the mechanism in question is one that a biological entity has on its own. An external mechanism, by contrast, is not intrinsic. Among other things, an external mechanism is not a property of the biological entity in question and is not under its control. In the context of the examples, these mechanisms are not just external, but also extrinsic. The reason is that two duplicate biological entities—to the extent that biological entities can be duplicates of each other—would not necessarily be under the effects of the same environmental factors in every different environment. Partly for that reason, I think that the terms “external” and “extrinsic” can be equated in this scenario.¹ However, to emphasize physical and ontological matters separately, I will reserve the term “external” for mechanisms and environmental factors and “extrinsic” for biological individuality or its supervenience base. If the supervenience base of biological individuality includes external mechanisms

¹However, I am unsure whether these terms can be equated *in general*.

in some scenarios, as I will argue, then there are cases where biological individuality is an extrinsic property.

3 Defining Properties and an Account of Biological Individuality

The properties typically used as criteria to distinguish biological individuals from other entities exhibit striking variation. Some examples range from being a product of sexual reproduction (Carpenter 1848; Huxley 1852; Janzen 1977), to being spatially and temporally localized (Hull 1980), causally integrated (Sober 1991), being genetically homogeneous and unique (Santelices 1999), showing some kind of autonomy (Wilson 2005), possessing an immune system (Pradeu 2012; 2013), or having reproductively specialized parts (Godfrey-Smith 2009; 2013). Many of these examples are intrinsic properties, but not all. As a reviewer has remarked, being the product of sexual reproduction and being genetically unique are not.² Much more exhaustive samples of properties, where similar distinctions could be made, can be found elsewhere. Depending on where one looks, the count can go from fifteen (Clarke 2013, 415) up to twenty-four different defining properties (Lidgard and Nyhart 2017, 19). Some of these have been used in isolation, as sole distinctive markers of individuality. Most, however, are now employed in various arrangements (i.e., Wilson 2005; Godfrey-Smith 2009).³

To make a point about the nature of biological individuality, in the sense that I pursue in this paper, one has to start from one account or another. The problem is that many accounts of biological individuality offer conflicting and non-coextensive results for the very same cases (Clarke 2010; Lidgard and Nyhart 2017). Where one account claims that there is a biological individual, another says there isn't. An account that offers a synthesis of various seemingly incompatible views is Clarke's (2013). Among other things, her account unifies multiple different accounts of biological individuality by advancing a functional perspective (429). This is the account I will work with going forward. Due to its synthetic and functional approach, the account provides one of the most comprehensive bases for claims about the nature of biological individuality. To the extent that Clarke's synthesis is successful, I will assume that my arguments *indirectly* hold for many of the subsumed accounts as well.

Clarke (2013, 2016a) has defended an evolutionary account of biological individuality based on a functional approach to the properties that work as criteria. As other evolutionary takes on biological individuality have done (Godfrey-Smith 2009), hers "assumes that the properties relevant to being an organism are just those properties that determine the extent to which, or the efficacy with which, *natural selection can occur*" (Clarke 2013, 427; emphasis mine). Put another way, a biological entity is an individual only if it has mechanisms that allow it to participate "in a selection process, that is, that give it the capacity for *heritable variance in fitness*" (430; emphasis mine).⁴ This reliance on mechanisms grounding the capacity of an object to participate in selective processes has an important consequence, although one not necessarily tied with individuals themselves.

One of the features of Clarke's account is that it unifies seemingly conflicting, and sometimes even non-coextensive definitions by offering a functional interpretation of the properties

²In like manner, if one holds an extended view of cognition, and autonomy (Wilson 2005) is a mind dependent property, then this property isn't necessarily intrinsic either.

³This passage is meant as a description of various accounts of biological individuality, but it is not necessarily an endorsement of the idea that there is, in fact, a single correct combination to be found.

⁴Clarke's most recent elaboration of the account (2016a) contains a slight twist, which nonetheless seems to follow what was contained in the earlier presentation of the account (2013). Whereas the earlier take (2013) emphasizes *selection* as the determinant process, the later one concentrates on *evolution* (2016a, 903, 909). However, there might be reasons to distinguish them.

associated with them (2013, 413). Instead of focusing on actual mechanisms (such as bottlenecks, germlines, immune systems, integration processes, and so on), Clarke concentrates on what these mechanisms *do* from an evolutionary point of view. In doing so, she notices that actual mechanisms are alternative realizers of functions common throughout the biological world. While some organisms rely on germlines to inhibit selective conflicts on lower levels of organization, others do just as well via modular structures and rigid cell walls. As long as a biological entity has a mechanism performing the relevant function, it does not matter if it is one or the other. In this sense, the functions that matter for biological individuality are *multiply realizable*. I will now deal with the mechanisms that Clarke deems necessary and sufficient for biological individuality together with their respective functions.

3.1 Policing and demarcation mechanisms

Selection between entities at the same level of organization is a common occurrence in evolutionary processes. When it comes to individuality, however, the processes that matter usually involve selective processes happening simultaneously at various different levels. This circumstance presents an issue for the evolution of individuals located at higher levels of organization, such as multicellular organisms (Michod 2011, 184). The issue is that when selective processes in lower levels are left on their own, individuals at higher levels cannot evolve (Okasha 2006, 223). For this and other reasons, inhibiting selective conflict among lower-level units is a necessary step in some evolutionary transitions (Buss 1987; Maynard-Smith and Szathmary 1995; Michod 2011).

The first kind of mechanism that Clarke deems necessary for biological individuality deals precisely with these sorts of conflicts. Biological individuals must possess policing mechanisms, namely “any mechanism that inhibits the capacity of an object to undergo within-object selection” (2013, 421). Some actual mechanisms that can perform this function are those that partially de-Darwinize lower-level entities. Both bottlenecks and germlines do so (Godfrey-Smith 2011, 76). The first inhibits within-object selection by reducing genetic variance between constituent cells. The second realizes the *same* evolutionary function but does it by depriving cells of one of the aspects of fitness (either viability or reproduction), thus precluding them from participating in selective processes on their own.

However, it would be wrong to think that policing mechanisms are sufficient to make something an individual. Notice that policing mechanisms, as Clarke mentions, are “wholly negative” (2013, 423). They deal effectively with the level below, but remain silent about the higher level of selection, which is presumably where the individual of interest would be found. In order to be an individual, a biological entity “must have a positive capacity to undergo natural selection at its own level” (423). I now turn to the mechanisms in charge of this capacity.

An intuition ingrained in various corners of the debate is that individuals have to be different from each other in relevant ways. In some instances, the purported difference is genetic. Individuals are sometimes thought to have a unique genotype (Santelices 1999; Janzen 1977). In other cases, there is no reference to genes, but the idea that something distinguishes one individual from another still lingers. Hull (1980, 1992), for example, believed that individuals had to have distinct spatial and temporal boundaries, an idea that has been specified in various ways in recent years (Pradeu 2012).

Clarke accommodates this intuition about differences within her scheme but does it with a functional twist that has evolutionary processes in sight. In addition to policing mechanisms, biological individuals must possess mechanisms capable of increasing or maintaining “the capacity of an object to undergo between-object selection” (2013, 424). These are demarcation

mechanisms. To see how they work, consider an example. By tying genotypes in new combinations, sexual reproduction *increases* “between-organism genetic variance” (Clarke 2013, 424), thereby intensifying the force of selection among higher-level entities in a population. As a result, sexual reproduction endows individuals with evolutionarily relevant differences. Similar difference-endowing outcomes can be achieved through other means. Polyploidization in plants and lateral gene transfer in bacteria can be counted as additional instances of demarcation mechanisms (426).

One potential problem for organisms and their selection-enhancing differences is that these can be lost. If the interactions between different collectives involve component migrations and exchanges of various sorts for long enough, then the risk of two distinct collectives merging into one suddenly becomes possible. Higher-level entities therefore require some mechanisms to deal with circumstances that threaten to erase relevant differences. Spatial boundaries and inter-colony aggression (426) typically perform this *maintenance* function. They help preserve selective differences by “preventing mixing or migration between” higher level entities (425).

3.2 *The possibility of external mechanisms and an intrinsic commitment*

The main outcome of Clarke’s account is a definition that specifies membership conditions for the class of biological individuals by way of necessary and sufficient conditions.⁵ According to Clarke, biological individuals are “*all and only* those objects that *possess* both kinds of individuating mechanisms” (427; emphasis mine). A biological entity is an individual by virtue of having both policing and demarcation mechanisms. There are good reasons to believe that familiar biological individuals own these mechanisms, as I will suggest later. But as Clarke duly notes, unfamiliar scenarios hint at an alternative. Consider the early stages of an evolutionary transition in individuality. In those circumstances, the individuality of higher-level entities is not entirely secured, as most of the mechanisms that could effectively enforce their individuality have not evolved yet. However, this doesn’t mean that these entities are just loose collectives. Clarke suggests that individuals in early transitional stages could forgo possessing “individuating mechanisms intrinsically—within their own skins, so to speak” (2013, 427n53). It may be enough “for the mechanisms to exist in the environment, so long as they are stable enough that their effect is heritable” (427n53). What does this possibility mean for biological individuality? If the mechanisms that ground biological individuality can be external to biological objects, then biological individuality won’t be tied purely to features *of* those objects. In those scenarios, biological individuality is not necessarily an intrinsic property of biological entities.

Despite this possibility, Clarke (2016a) has opted for a different path. In the most recent elaboration of her individuality account, she contends that “individuality ought to be intrinsic to the unit in question” (900). If individuality were not intrinsic, she argues, the property would be “hostage to facts which [have] nothing to do with the unit in question—facts about population size and about the environment, as well as sheer luck” (900).⁶ This commitment to the intrinsic stance I think reflects a wider trend in the existing literature. The idea that individuality supervenes on the intrinsic properties of biological entities seems to be common assumption. Most individuality accounts are ultimately based on properties that are intrinsic. Integration, germlines, and immune systems are just a few of them (i.e., Godfrey-Smith 2009; Pradeu 2012). As Chiu and Eberl (2016) observe, criteria of biological individuality “are usually

⁵As Clarke comments in one of her footnotes, this is the aim of her account: “the problem I treat here is one of finding necessary and sufficient conditions for membership of the class” (2013, 414n6).

⁶For this and other reasons Clarke prefers accounts that decide individuality cases based on the capacity of an object to participate in selective or evolutionary processes, in contrast with positions that consider “the actual proportion of selection at the focal level” as what “constitutes evolutionary individuality” (2016a, 901).

‘inward-looking,’” and tend to draw “sharp [distinctions] between internal interconnection on the one hand and organism–environment interactions on the other” (829). Thus, “only features of the internal and the boundary that mediates the inside with the outside seem to be important for individuality” (829).

There are various reasons that, in conjunction, could explain the appeal of the intrinsic stance. Some derive from our contact with paradigmatic or familiar biological individuals, such as mammals or vertebrates. One feature of familiar biological individuals is that they maintain their individuality even in changing surrounding conditions. From the standpoint of their individuality, the environment they find themselves in or whether members of their populations come and go doesn’t make much of a difference. They are still individuals. Even when they die, they are dead individuals. Familiar biological individuals appear to ‘carry’ their individuality with themselves. Given these circumstances, there is ground to think that something *about* those entities makes them individuals.

Other reasons are not tied directly to individuality. Yet, they underscore the importance of intrinsic properties for significant biological features. One example is the connection between intrinsic properties and evolutionary potential. According to Godfrey-Smith, paradigmatic Darwinian populations—the kind of populations that go through adaptive evolution—are characterized in part by a high dependence of realized fitness differences on intrinsic properties or characters (2009, 53–6).⁷ Some have expressed doubts about this idea as it stands, but believe it can be salvaged by thinking about it in terms of heritability and developmental control (Sterelny 2011, 498). Kim Sterelny has emphasized that high heritability, which is at the base of cumulative selection, requires having control of phenotypic development. This is so because “the more development is affected by environmental noise and disturbance, the less reliable offspring resemble their parents” (498). In processes of adaptive evolution, “the boundary of the agent is often the boundary of reliable developmental control” (498). This kind of control is something that members of paradigmatic Darwinian populations have. Familiar biological individuals are typically members of these populations and are products of adaptive evolution. As with other relevant biological features, perhaps their individuality depends on intrinsic properties as well.

Finally, there are reasons to hold an intrinsic view about biological individuality that can be traced back to metaphysics. One salient approach to natural kinds suggests that these are defined by their essential properties (Putnam 1975; Kripke 1980). An aspect of this framework is that “natural kind essences must be intrinsic” (Tahko 2015, 800). Biological individuals seem to be a natural kind, or at least they have been treated as such. It wouldn’t be surprising if the efforts to find a definition of biological individuality had this particular view working in the background. In that framework, intrinsic properties are key.

There are many different reasons to believe that the individuality of biological entities has a purely intrinsic base. This is likely to be the case for most familiar biological individuals. However, I think there are grounds to believe that individuality isn’t always intrinsic. In the next section, I explore the possibility of individuality determining properties that are not bounded to biological individuals. In particular, of external factors acting as individuation mechanisms. I suggest that certain environmental factors can fulfill some of the functional roles that Clarke envisioned in the early stages of evolutionary transitions.

⁷This is one of the parameters that Godfrey-Smith has proposed to distinguish marginal, minimal, and paradigmatic Darwinian populations (2009, 63–4). The parameter, *S*, has also been fleshed out in terms of supervenience. It measures “the degree to which the difference-makers with respect to reproductive success *approximate* being supervenient on the intrinsic character of the members of the population” (55).

4 External Mechanisms

The importance of environmental conditions for individuality began to be noted in recent years (Ereshefsky and Pedroso 2015b; Hanschen et al. 2017; Black et al. 2019). One recurrent question is whether Darwinian properties, namely, those that allow entities to participate in selective processes, *can* be bestowed on entities by external or environmental processes (Ereshefsky and Pedroso 2015b; Black et al. 2019). In this section I intend to answer a factual variant of that question with a particular range of cases in sight. The question is whether *there are* external mechanisms that can determine the capacity of an object to undergo selection. Note that in this context the capacity to undergo selection is tied to the heritable variance in fitness of biological entities (Lewontin 1970). Since those are the properties typically affected by individuation mechanisms, the issue falls under the scope of the debate about evolutionary individuality (Clarke 2013). This section provides an answer to the question by way of two examples. Both of them resemble early transition stages, partly because the individuality of the collectives involved can be controversial. The first case concerns biofilms, whereas the second involves snowflake yeast clusters.

4.1 *Ecological disturbances in biofilms*

It is not uncommon to picture microbes living somewhat lonely lives. However, microbes in natural environments tend to live lives that are far from solitary (Clarke 2016b). Unlike some of their imagined counterparts, they are usually found inside cohesive and intricate communities comprised by clusters of various cells (Ventura 2019, 1). These single or multispecies communities tend to exhibit quite complex features. The repertoire includes a “well-defined cell organization and a functional division of labor” (Dupré and O’Malley 2009, 11), persistent interactions among cells, and collaborations of various sorts, including metabolic ones (11). Complex bacterial aggregates characterized by these features are commonly known as biofilms.

Biofilms form through a process in which various bacteria, sometimes of different species, coaggregate by attaching to one another (Rickard et al. 2003, 94; Ereshefsky and Pedroso 2015b, 104). A feature that differentiates biofilms from loose cell aggregates is that they collectively construct and live within an extracellular matrix (ECM) (Clarke 2016b, 192). This matrix performs various roles. It physically holds the cells together, but also acts as a digestive system (Ereshefsky and Pedroso 2013, 332): nutrients accumulate in the matrix while extracellular enzymes grind them into manageable pieces (Ereshefsky and Pedroso 2015b, 104; Fleeming and Wingender 2010). Another salient characteristic of biofilms, similarly facilitated by the ECM, concerns the kinds of interactions between cells. Cells in a biofilm tune their phenotype as a response to population density (Clarke 2016b, 193) thanks to a cell-to-cell signaling system called quorum sensing (Ereshefsky and Pedroso 2013, 333). But they do more than that. Biofilm constituents genetically blend themselves, at least to some extent, by exchanging genes through lateral gene transfer (333).

Partly because of this complex repertoire of traits, the status of biofilms as either ecological communities or individuals has been a focus of debate (Ereshefsky and Pedroso 2013; Ereshefsky and Pedroso 2015a; Clarke 2016b). I do not intend to meddle in that debate. What the example I am about to suggest requires is that biofilms figure somewhere along the continuum of evolutionary individuality. All I need is that the case for biofilms’ individuality is not *entirely* ruled out. That appears to be the current situation (Clarke 2016b). The goal of the next example is to show how environmental factors can spur individualization in biofilms. Some of the details involve mass mortality events and a substantial reduction of selective conflicts among biofilm members.

4.2 *Ecological disturbances as external policing mechanisms in Pseudomonas fluorescens*

Public goods are a common feature of microbial worlds (Brockhurst et al. 2010, 334). In the context of biofilms, a public good is a “product that is costly to produce and enhances the fitness of other cells” (Ereshefsky and Pedroso 2015a, 10127). The ECM is an example. These products are usually made by cooperator cells which incur in relatively high metabolic costs, even though they benefit all the cells in the ensemble (Brockhurst et al. 2010, 334). Along with cooperator cells, there are also cheating ones, which benefit from public goods without producing them. Because of that circumstance, cheating cells typically enjoy a fitness advantage over cooperators (334). The question is how this kind of cooperation, widespread in biofilms, can be maintained in the face of free-riding cheats (Ereshefsky and Pedroso 2015a, 10127). One answer points to the environment (10127).

Brockhurst, Buckling, and Gardner (2007) suggest that external, environmental factors might be doing some of the work. They have shown experimentally that ecological disturbances can cull the percentage of cheaters inside a biofilm.⁸ Ecological disturbances are “nonspecific mass-mortality events” that severely reduce the numbers of a group or population (762). The broad picture gathered from the experiments is that events such as these “can create conditions that retard the breakdown of cooperation within a microbial social group in the absence of other more complex, supporting mechanisms” (Brockhurst et al. 2007, 765).⁹ I now turn to the details.

The experiments involve two morphs of *Pseudomonas fluorescens*. Cooperators of the wrinkly spreader (WS) genotype form a biofilm at “the air-broth interface through constitutive overproduction of cellulosic polymer” (762). This constitutes a public good because it gives the biofilm “access to oxygen, a limiting resource” (762). Non-cellulose-producing cheats of the smooth spreader genotype (SM), on the other hand, arise through a “loss-of-function mutation” and enjoy the benefits of inhabiting the interface-niche without collaborating with the products that sustain the biofilm (761). Because they incur fewer costs, the growth rate of SM cheats is higher than WS wild types within the biofilm. This situation severely compromises the integrity of the biofilm: cheats add weight without strengthening the structure of the biofilm through cellulosic products (761).

What Brockhurst et al. (2007) found is that the proportions of cheats vary with different frequencies of external ecological disturbances. In the context of the experiment these involved discarding 99.9% of the population and moving what remained “to a fresh microcosm” (762). Cheaters predominate if the mass-mortality events occur too often (762). The reason is that under frequent disturbances, the biofilm never reaches a density threshold “above which cooperation provides a group benefit” (761). A similar outcome ensues when disturbances are sparse. In this case the biofilm reaches the density threshold, but it is overrun by cheats that arise by mutation (761).¹⁰ When disturbances occur at an intermediate frequency, however, cooperation predominates. Brockhurst et al. noticed that “the proportion of [WS] cooperators within a population displayed a unimodal relationship with disturbance frequency, peaking at intermediate rates” (762). The conclusion is that “intermediate frequency disturbance can forestall the breakdown of cooperation” (762).

Here ecological disturbances work as instances of external individuating mechanisms. Ecological disturbances at intermediate frequencies externally foster cooperation within a biofilm

⁸Ecological disturbances have also been shown to impact the diversity of species in various ecosystems (Petraitis et al. 1989; Buckling et al. 2000).

⁹They mention policing mechanisms, punishment, reciprocity, and character displacement among more complex mechanisms.

¹⁰This assumes that the rate of mutation that turns WS into SM is higher than the other way around (763).

by *reducing selective conflict*. They do so partially by giving populations of cells enough time to grow up to a density in which cooperation is useful (763). However, there is a second effect that, although associated with the first one, is more important for the case I am trying to advance. Frequent enough disturbances *reduce genetic variance* within a biofilm by imposing an ecological bottleneck (763).¹¹ When mass mortality events are significant, most constituent cells die, and the biofilm is subsequently repopulated by a single or very few cells (763). Because a reduction in genetic variance dwindles the available fuel for selection, there are grounds to believe that, at least for a while, selective conflicts will diminish. This is precisely the sort of outcome we would expect from a policing mechanism (3.1). Yet, in this scenario the policing function is not driven by a feature *of* the biofilm. It is an external, environmental factor that is carrying the function. I suggest we understand these and other similar cases as instances of external policing mechanisms, just as Clarke had envisioned them (2013, 427n53).

4.3 Cell death and group formation in snowflake yeast clusters

As the previous section, this one explores a case in which environmental factors can perform roles that fulfill Clarke's descriptions of individuating mechanisms. The focus, again, is on circumstances that highlight the impact some environmental challenges can have on the evolution of group formation and common goods (Gulli et al. 2019, 1019). Although biofilms are typical case studies (Brockhurst et al. 2010), other biological entities also engage with their environments in ways that might be relevant for individuality. For instance, Gulli, Herron, and Ratcliff (2019) have recently shown how cell death can promote aggregation between clusters of snowflake yeast. Before describing the details associated with this example, I will say a few things about aggregation with an emphasis on features that make it evolutionarily relevant.

Group formation is a crucial piece in the evolution of multicellularity (Herron 2017, 70). For multicellular individuals to evolve, something has to ensure that constituent cells attach to one another and remain so (Folse and Roughgarden 2010, 468). Staying within a group formation offer various benefits to formerly single-celled participants. These include protection from predators (452), thermal insulation, and the ability to exploit environmental resources that would be otherwise out of reach (Gulli et al 2019, 1012). The early stages of simple multicellularity¹² commonly involve adhesion (daughters cells stay glued together post division) or aggregation (single cells coming together) (Radzvilavicius and Blackstone 2018, 1628). Once initial steps have been reached, other mechanisms can evolve to tighten the links of the group, such as the formation of extracellular matrices in volvocine algae (Herron 2017, 70).

Interactions that leave some cells tied to others are relevant for individuality in various ways. For example, they increase integration by forcing cells to "share an environment in which each is affected by the others' physiological activities" (72). Integration in its numerous forms has for long been deemed a distinctive mark of biological individuality (Lidgard and Nyhart 2017, 23). From an evolutionary point of view, there is a consequence of group formation that is particularly important for individuality. Grouping matters because it can align the fitness interests of its participants (Herron 2017, 78). Given that cells tied together tend to experience the same environments and usually succeed or fail together, group formation at earlier stages of a transition can be seen as a way of diminishing fitness differences (78). In particular, interdependencies generated by gluing cells together impose a constraint over the fitness outcomes that

¹¹An example of an ecological disturbance causing a bottleneck could be an antimicrobial treatment, as Ereshefsky and Pedroso (2015a, 10129) have suggested.

¹²That is, groups without internal differentiation.

participants can enact. Thus, different strains that depend on each other are “not free to evolve independently” from one another (Clarke 2016b, 205).

Recent experiments illustrate how cooperation and certain forms of grouping between snowflake yeast clusters can evolve in adverse selective environments (Gulli et al. 2019). One feature of snowflake yeast is that they tend to form branching clusters of genetically related cells (1013). The branching pattern of growth can be explained by the fact that clusters “arise via post-division adhesion” of daughter cells, and “not by aggregation of previously separate cells” (Ratcliff et al. 2012, 1596). Daughter cells that remain attached combined with rigid cell walls give snowflake yeasts their particular figure. There is, however, more than branching clusters to snowflake yeasts. When certain environmental resources are available, other grouping structures become possible.

Gulli and colleagues’ experiments on snowflake yeast have shown that when solitary cluster lifestyles are selected against,¹³ larger aggregates of a “tangled, ropelike appearance” containing hundreds of clusters begins to form through the production of a common good (Gulli et al. 2019, 1013). What the experiments suggest is that initially lone clusters of snowflake yeast can group into proteinaceous aggregates if certain conditions are met. According to Gulli et al., aggregates appear to be a side-effect of proteins being liberated from lysed cells that were once members of clusters with “high rates of programmed cell death” (1019). In order to assess the connection between the formation of aggregates and cell death, Gulli et al. induced cell death on cluster strains by exposing them to hydrogen peroxide (H_2O_2). They found that populations of clusters exposed to H_2O_2 “formed aggregates earlier [...] and more frequently than unexposed populations” (1017). These results indicate that, by liberating proteins that act as building blocks, cell death can promote the formation of proteinaceous aggregates between snowflake yeast clusters (1017).

4.4 *Cell death as an external policing mechanism in snowflake yeast*

The formation of proteinaceous aggregates in these experiments has an identifiable internal cause. Programmed cell death, which is a feature of constituent cells inside clusters, is the difference-making cause. It kills cells at a certain rate, liberates proteins from former living members of the clusters, and enables aggregate formations to appear. Although these details are well established, there are grounds to think that other factors, perhaps environmental, might perform a similar function. If what aggregates require is a stable amount of available proteins, we could expect an environmental factor decimating snowflake clusters at a regular rate such that it liberates enough proteins in a population for aggregates to form.¹⁴ Predation probably will not do, since proteins tend to be consumed, but other factors might kill cells and leave proteins around. After all, in nature death is everywhere.

I think that environmental mechanisms realizing that function would count as external policing mechanisms (Clarke 2013). As suggested in previous sections, mechanisms responsible for aggregation or other sorts of grouping end up tying together the fitness of lower-level constituents, to the extent that is possible, by ensuring they experience similar environments (Clarke 2016b, 205). By reducing fitness variance among constituents, such mechanisms effectively diminish selective conflicts. One disadvantage is that external mechanisms driving aggregation through death may not be as effective, robust, and regular as bottlenecks or germlines. Gulli et

¹³The experiment involves selecting for settling rate. Lone clusters take longer to settle, whereas aggregates have a selective advantage by settling faster (Gulli et al 2019).

¹⁴A group of biologists killing the cells directly, instead of inducing cell death, could count as an instance of these external mechanisms.

al. observed that even with relatively high rates of apoptosis, the cells within snowflake yeast aggregates are not clonal nor nearly so (205). However, such mechanisms still manage to grapple with low-level variance, specifically fitness variance, in a way that might benefit the aggregate level, even if their effects are not particularly reliable or long-lasting. Once some sort of stability has been achieved at the aggregate level, more robust and efficient mechanisms can evolve and take over.¹⁵

Up to this point I advanced an argument for the existence of external individuation mechanisms. That is, of mechanisms whose functions are decisive for the individuality of biological entities. I did so, firstly, by showing how ecological disturbances affecting biofilms can be seen as an instance of them (Brockhurst et al 2007). Secondly, I introduced an actual scenario in which possible external individuation mechanisms can fulfill the role of empirically observed internal mechanisms (Gulli et al. 2019). Cell death in snowflake yeast clusters can produce aggregation by liberating proteins, which in turn serve as a grouping resource. Because both ecological disturbances and environmentally induced cell death manage to reduce selective conflicts at lower levels of selection, I argued that they are examples of external factors working as policing mechanisms (Clarke 2013).¹⁶

Establishing the existence of external individuation mechanisms by way of examples is crucial because it upholds the main argument against the intrinsic stance. The main argument, initially advanced only tentatively, is that individuality—evolutionarily conceived—is not necessarily an intrinsic property of biological entities. Put another way, the argument holds that biological individuality is not always held by features *of* the entities counted as individuals. Although the intrinsic stance appears to be a common assumption within the debate, I think biofilms and snowflake yeast aggregates offer an antidote against it. In cases like these, biological individuality partly supervenes on the activity of external mechanisms. Whenever this is the case, biological individuality will not be a purely intrinsic property. This is so because very similar biological entities will not be affected by these or other types of ecological disturbances in every different environment. One biological entity in a particular environment where these ecological disturbances occur may be an individual. By contrast, a very similar biological entity in a different environment where ecological disturbances are absent won't be. For certain kinds of biological entities, biological individuality is a property that can be present or absent in physical duplicates.

The connections between these examples and the main argument, however, may not be as reliable as I portrayed them. The next section is intended to deal with doubts about the

¹⁵There is another potential role for cell death sources in snowflake yeast cluster aggregates. Because these form branching structures of daughter cells glued together, the death of cells along a branch can trigger a process of marginal reproduction at the aggregate level through fragmentation and the imposition of an external bottleneck. Thus, some kind of aggregate-level reproduction could be enacted by an external source. A similar scenario has been suggested by Kerr and Rainey (2011) for the reproduction of biofilms through the collapse of biofilm mats either due to internal causes (i.e., overrun by cheater strains and free-riders) or external factors (i.e., a “stochastic disturbance of the broth in which the mats grow” 149).

¹⁶These examples show that certain ecological disturbances can exert the same individuation functions that Clarke's policing mechanisms have. One question is whether the ecological disturbances that perform these functions are mechanisms in a general sense. To the extent that ecological disturbances involve entities and activities organized in a way that makes them responsible for certain phenomena, they satisfy a well-known synthesis view about mechanisms and could be regarded as such (Illari and Williamson 2012, 120). A different question is whether the effects of ecological disturbances or other external factors are as reliable, robust, or long-lasting as those of highly evolved individuation mechanisms. As I see it, these properties have more to do with the degree of individuality these mechanisms can bring about, and not so much with whether they are individuation mechanisms at all. This issue is largely a matter of degrees and would have to be settled in a case-by-case manner. I thank the reviewers for highlighting these issues.

evidential support I assumed the examples can bring. I will also address some questions about the individuality of biofilms and snowflake yeast aggregates.

5 Doubts About External Individuation Mechanisms

There are reasonable doubts about the support that biofilms and snowflake yeasts can provide for the main argument, namely, that biological individuality need not be intrinsic. The examples employed and the features emphasized, it may be objected, are insufficient on their own to establish that biological individuality can be partly constituted by external mechanisms, or put another way, that there can be external mechanisms in the supervenience base of biological individuality. Part of these doubts stems from the allegedly external character of the mechanisms in the examples. Because the main argument requires mechanisms to be external in a particularly strong sense, not every function performed by these external mechanisms will do. If the environmental factors in the examples were mere scaffolds to internal individuation mechanisms, for example, then they would not warrant negative claims about the intrinsic character of biological individuality. The aim of this section is to tackle an objection that gives form to these doubts. I will attempt to dismantle the objection by showing how features of the mechanisms involved in biofilms and snowflake yeasts examples can substantiate the argument against the intrinsic stance.

The objection against the main argument goes like this. It is not entirely clear whether the empirical details associated with both biofilms and snowflake yeasts aggregates serve as evidence for the claim that biological individuality isn't necessarily intrinsic. On the contrary, it seems that the evidence offered actually supports a much weaker position. The core of the main argument can be formulated in the following way:

- (i) To be a biological individual, an entity must, as a matter of necessity and sufficiency, possess a certain set X of properties. However, some of these properties can be external.

The set of properties corresponds to Clarke's policing and demarcation mechanisms. What I argued throughout this paper is that concrete realizations of those mechanisms can be external to the biological entities in question. Now consider a different and arguably weaker claim:

- (ii) To be a biological individual, an entity must possess, as a matter of necessity, a certain set X of properties; and empirically, the causal explanation of why an organism exhibits one or more of the properties in X involves the external environment.

The main issue for the line of argument I have developed is that (ii) could be true even if the individuating mechanisms in X were all intrinsic. This alternative reading suggests that the factors I have identified as external individuation mechanisms are not so. Instead, they should be conceived as scaffolds of some sort, as mechanisms that support the development or function of the properties in X . The properties or mechanisms in X are those that biological entities possess. If that were the case, then biological individuality would remain as a purely intrinsic affair. Individuality would still supervene solely on the intrinsic properties of biological entities. In order to defend the main argument, I have to show how the empirical evidence examined in earlier sections supports (i) rather than (ii). The idea behind (i) is that, in some cases, the supervenience base of biological individuality can include external mechanisms. To defend this idea, I go back to the examples introduced in earlier sections with a few additions. The answer relies on relevant features of both biofilms and snowflake yeasts, but contrasts these with the role

that resident microorganisms have in the immune capacities of some biological entities (Chiu and Eberl 2016). I will suggest that the difference between these cases can be understood as differences between external and scaffolded mechanisms.

In a relatively recent paper, Chiu and Eberl (2016) argued that resident microorganisms can act as scaffolds for certain immune capacities of their hosts. Among other effects, the presence or absence of these microorganisms has a significant influence on the regulation of immune responses in host organisms, an influence that ranges from enabling to inhibiting that activity (9). The key point from an individuality perspective is that immune systems are instances of policing mechanisms (Clarke 2013). What Chiu and Eberl's examples show is that there are cases of scaffolding in which external factors can have a significant causal impact over the operation of intrinsic policing mechanisms, even though those factors are not policing mechanisms themselves. In this particular scenario, I think that the immune system can be conceived as an intrinsic scaffolded mechanism. Scaffolded mechanisms are intrinsic to biological entities, but their development or functioning requires substantial external influence and support. This I think is a variant of the scenarios depicted by (ii). Although there is an intricate causal story involving microorganisms that explains why the host's immune system works as it does or acquired the state it has, the immune system remains as an intrinsic property that partly grounds the host's biological individuality.

But what about the mechanisms in other examples? Consider the biofilm case. Because the external mechanism that realizes the individuation function is not, as far as I know, supplanting any intrinsic equivalent,¹⁷ the support this example brings to (i) is much clearer. Ecological disturbances act as policing mechanisms by imposing an ecological bottleneck over biofilms, which results in a reduction of both genetic variance and selective conflicts at lower levels of organization. Instead of causing the development of a policing mechanism inside the biofilm or scaffolding the function of an intrinsic mechanism already present, ecological disturbances exert an individuation function from the outside and retain their status as independent policing sources. This causal behavior and its consequences give us good reasons to regard ecological disturbances as concrete instances of policing mechanisms. If they are, then ecological disturbances are as constitutive of biological individuality as any other policing mechanism (Clarke 2013), in spite of not being possessed by the entities that gather our interest. Such external mechanisms and their effects represent adequate realizations of the scenarios considered by (i) and therefore work in favor of the main argument against the intrinsic stance.

Snowflake yeast aggregates, on the other hand, appear to offer a somewhat ambivalent or intermediate case. This is due in part to the role played by programmed cell death or apoptosis in the formation of aggregates. As stressed in earlier sections (4.3), programmed cell death is causally responsible for the liberation of proteins, which in turn allows snowflake yeast clusters to entangle others and form larger proteinaceous ensembles. This property, however, is ultimately an intrinsic property of living cells that comprise various clusters. So even if programmed cell death was scaffolded or induced by factors external to snowflake yeasts, the mechanism driving the individualization process would maintain its intrinsic character. In that particular scenario, programmed cell death would count as a scaffolded mechanism. Thus, snowflake yeast cluster aggregates would serve as empirical evidence for (ii) instead of (i).

There is an alternative path, however. A different source of cell death could make a substantial difference for the kind of support provided by the snowflake yeast example. If the main source of cell death was not apoptosis but something else entirely, then this case may slide towards (i). To count as evidence of (i), there has to be an external source of cell death capable of supplanting—not merely inducing or supporting—the function of apoptosis in aggregation.

¹⁷Some sort of internally induced bottleneck.

That is, there must be an external mechanism killing cells directly, not just scaffolding an intrinsic mechanism with the same function, such as programmed cell death. Any mechanism doing so would be a functionally equivalent but external policing mechanism. Perhaps ecological disturbances or any other death event capable of liberating proteins at a certain rate could do the trick.

As a reviewer has pointed out to me, there are clear parallels between this objection and an objection that has been levelled against extended views of cognition (Clark and Chalmers 1998; Wilson 2010). According to these views, the processes and states that constitute cognitive systems “physically extend beyond the boundary of the individual agent” (Wilson 2014, 19). The idea is that certain external objects, processes, and mechanisms can be proper parts of cognitive systems due to how they contribute to the functions of those systems (Clark 2010). A notebook, for example, can work as an external memory storage device, which can serve various cognitive tasks. To that extent, cognitive systems are extended. But not everyone agrees. A usual objection against advocates of extended views of cognition is that they perform a coupling-constitution fallacy (Adams and Aizawa 2010). The fallacy is to assume that because environmental factors are causally coupled with cognitive processes, those factors are proper parts of such processes and that, therefore, cognition systems are extended. Usually, the objection is raised by internalists about cognition. Internalists claim that although cognition can be influenced by external factors, it ultimately “supervenes on the intrinsic, physical properties of the individual” (Wilson 2014, 19).

Like the objection put forward by internalists against extended views about cognition, the (ii) objection raised in this section downplays the functional significance of external factors. In this case, in regards to the individuality of certain biological entities. If (ii) were the case, then the supervenience base of individuality would be purely intrinsic. External factors like ecological disturbances would be just scaffolds to the development or the activity of intrinsic individuation mechanisms. There would be significant external influences, but all the defining factors would be within the boundaries of the individuals. That’s a parallel between the objections against extended cognition and (ii). But there are some disanalogies. Note that my argument is not a fully-fledged extended view about individuality. I don’t conclude that individuality is extended. However, the existence of external individuation mechanisms can work as a prelude for views of that sort.

6 Doubts About the Individuality of Biofilms and Snowflake Yeast Aggregates

The case developed so far against the intrinsic stance can be contested on somewhat different grounds. One might accept the existence of external individuation mechanisms but reject that biofilms and snowflake yeast aggregates exhibit some kind of individuality. It’s not the character of the mechanisms that is in doubt, then, but the individuality of the biological entities in the examples. I will approach this objection by considering each of the examples in turn.

The individuality of biofilms has been debated in recent years. In a series of papers, Ereshefsky and Pedrosa (2013; 2015a; 2015b) argued not just that biofilms should be regarded as evolutionary individuals, but that some of their peculiarities should lead us to rethink our general views about evolutionary individuality. Biofilms have many of the features typically associated with individuals, such as integration of some sort, a division of labor between parts, and even heritable adaptive traits. However, as Ereshefsky and Pedrosa (2015a) emphasize, biofilms lack many of the concrete features that are often expected of evolutionary individuals. These include going through reproductive bottlenecks and forming unified reproductive lineages.

In part due to these circumstances, some have put the evolutionary individuality of biofilms in doubt (Clarke 2016b). Yet, there is some nuance in the case against biofilms' individuality. After Ereshefsky and Pedroso's (2013; 2015a; 2015b) detailed defense of biofilms' individuality, what seems to be in question is not whether certain single-species biofilms, in particular circumstances, might count as individuals. What's doubtful is whether wild, multi-species biofilms in general exhibit *heritable* variance in fitness (Clarke 2016b, 198). The nature of aggregation in biofilms and the reproductive independence that some of the member cells maintain suggest that "there will rarely be enough genetic heritability across biofilm generations to support a response to selection" (208). Therefore, the question is whether wild multi-species biofilms can respond to selection to a degree that warrants considering them more than marginal evolutionary individuals (199). The answer to this question seems to be mostly an empirical issue: "for any particular biofilm there will be an empirical fact of the matter about the extent to which the aggregate responds, as a whole, to natural selection, as opposed to responding only at the cellular level" (208).

Some answers to these doubts have been proposed, however. Pedroso (2017) has suggested that the resilience of certain traits to changes at the genetic level, plus an evolutionary mechanism called recruitment, can ensure some degree of heritability at the biofilm-level. One aspect of biofilm co-aggregation is that it's not entirely open-ended (128). There are mechanisms that determine which species of bacteria will be recruited to co-aggregate into a new biofilm. But even if these mechanisms were to fail, certain abilities of biofilms like being able to cause caries are maintained even when some species are absent from the ensemble. As long as there is some heritability at the biofilm level, biofilms should be counted among those evolutionary individuals for which heritability is a defining feature.

As I mentioned in passing before, all the argument developed so far requires is that the individuality of biofilms isn't entirely ruled out. I've used biofilms as an example of biological entities whose individuality can partially supervene on external mechanisms. Discussions about biofilms' individuality suggest that at least some of them can be regarded as individuals (Clarke 2016b; Pedroso 2017). We might doubt the individuality of multispecies biofilms in the wild, but the individuality of single-species biofilms doesn't seem to be in question, at least not at large. Ereshefsky and Pedroso (2013; 2015a; 2015b) have given us good reasons to believe that at least some particular single-species biofilms can be considered evolutionary individuals. Now, it's certainly possible to claim that some single-species biofilms in particular, controlled environments are evolutionary individuals, but deny, at the same time, that they are paradigmatic evolutionary individuals. Biofilms don't seem to fit the standard views about paradigmatic evolutionary individuals (Godfrey-Smith 2009; Clarke 2013), but I don't think that would affect the argument negatively. What matters is whether biofilms can exhibit individuality at all. Put another way, whether they figure somewhere along the continuum of evolutionary individuality (Clarke 2016b, 198). That seems to be the case.

The individuality of snowflake yeast aggregates can also be challenged. But the question, in this case, is slightly different. The question is not whether they are paradigmatic evolutionary individuals, but whether they are individuals at all. Do snowflake yeast aggregates exhibit at least a minimal degree of individuality? The tools to figure this out have been introduced in some of the previous sections. A biological entity is an individual if demarcation and policing functions are performed, either by some of its own mechanisms or by external factors. In the case of snowflake yeast aggregates, I have argued that there are external factors capable of performing a policing function. Killing snowflake yeasts and liberating proteins allows proteinaceous aggregates to form, which reduces the fitness variance of lower-level constituents. That fulfills the policing function of the mechanisms that make certain biological entities also individuals.

What's missing is a demarcation mechanism. Recall that demarcation mechanisms are those that increase or maintain the capacity of an object to undergo selection at its own level (Clarke 2013, 424). A case of a very simple demarcation mechanism would be something capable of binding single cells with one another—for example, a mutation that glues formerly single cells into clumps (431). That would qualify as a demarcation mechanism because by having single cells stay together, such a mechanism “reduces slightly the capacity of cells to exhibit variance in fitness and shifts some of that capacity to clumps” (431). Note that in doing so, it performs both policing and demarcation functions. The fuel for selection at the lower level decreases, but it goes up at the higher level. These are the kind of individuation mechanisms we would expect to see in the very early stages of a transition in individuality, or in scenarios that resemble them.

But if such simple mechanisms can perform a demarcation function, then demarcation mechanisms are not missing from the snowflake yeast example. As I described previously, snowflake yeasts are able to form aggregates whenever proteins are liberated through lysis into the environment. They manage to form clumps at a higher level when proteins are available. If that is the case, then both policing and demarcation functions are being performed. Therefore, snowflake yeasts aggregates satisfy the minimal conditions of biological individuality.

All the same, one might still find these cases unconvincing. After all, the examples involve marginal biological individuals. They are marginal, among other reasons, because they resemble entities one might find in early transition stages, and because they figure in rather artificial scenarios. If someone were to believe that paradigmatic biological individuals are quintessential to any discussion about the nature of biological individuals, and in particular to the development of accounts and definitions of biological individuality,¹⁸ their absence could be grounds to cast doubt on the significance of these cases. The issue with such a view is that it restricts our understanding of biological individuality to its most salient examples. A comprehensive view of the nature of biological individuality, its evolution, and its development benefits from examples of all sorts, including marginal ones. The cost is that one has to pay attention to examples “that are recent, to the ones that are unconventional and even to the ones that are incomplete” (Queller and Strassman 2009, 3151).

7 Conclusion

The properties typically selected as criteria of individuality reflect a tendency to believe that biological individuality is an intrinsic property. In some cases, that idea has been openly defended (Clarke 2016a). As I suggested earlier, this is not some broad ontological point devoid of consequences. If we wonder about what makes something an individual, and we presume that biological individuality is a purely intrinsic affair, where will we look for answers? Assuming that biological individuality is an intrinsic property restricts the domain of relevant features in ways that are not justified. This is particularly true for evolutionary individuality. Neither the underlying theoretical tenets of evolutionary individuality accounts (Lewontin 1970) nor the properties involved therein demand that we limit our enquires to the boundaries of biological entities.

In this paper I argued against that general view about the nature of biological individuality. The main argument relies on Clarke's evolutionary account of biological individuality (2013) and a few examples that include entities in scenarios akin to early stages of evolutionary transitions. My key claim is that biological individuality can be extrinsic in some situations. This claim requires showing that properties or functions thought to be constitutive of individuality can

¹⁸I thank an anonymous reviewer for making this point much clearer.

be found beyond the confines of particular biological entities. The examples introduced are meant to do exactly that. Both biofilms and snowflake yeast cluster aggregates illustrate how environmental factors can prompt the individuality of biological entities by realizing functions usually attributed to intrinsic individuation mechanisms. Ecological disturbances and various sources of death offer a glimpse of what external individuation mechanisms can be. I think the cases examined and the mechanisms emphasized in them strongly suggest that biological individuality is not necessarily an intrinsic property.

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