**On Mycorrhizal Individuality**

This paper argues that a plant together with the symbiotic fungus attached to its roots, a *mycorrhizal collective*, is an evolutionary individual, and further, that mycorrhizal individuality has important implications for evolutionary theory. Theoretical individuation is defended and then employed to show that mycorrhizal collectives function as *interactors* according to David Hull’s *replicator-interactor* model of evolution by natural selection, and because they have the potential to engage in *pseudo-vertical transmission*, mycorrhizal collectives also function as Darwinian individuals, according to Peter Godfrey-Smith’s *Darwinian Populations* model of evolution by natural selection. Mycorrhizae in nature usually connect the roots of multiple plants, so mycorrhizal individuality entails the existence of overlapping evolutionary individuals, and because the potential to engage in pseudo-vertical transmission comes in degrees, it follows that these overlapping evolutionary individuals also come in degrees. I suggest here that the degree of evolutionary individuality in a symbiotic collective corresponds to its probability of reproducing with vertical or pseudo-vertical transmission. This probability constitutes a fourth parameter of graded Darwinian individuality in collective reproducers and warrants an update to Godfrey-Smith’s 3D model.

**1. Introduction**

Recent scholarship in philosophy of biological individuality has focused on *holobionts* (Margulis and Fester 1991), symbiotic collectives such as ourselves, each composed of one multicellular *macrobe* (Mindell 1992) together with all its associated microbes[[1]](#footnote-1). Margulis and Mindell, and more recently Zilber‐Rosenberg and Rosenberg (2008), Booth (2014a), and Bordenstein and Theis (2015), describe holobionts as evolutionary individuals. Objecting to this view, Godfrey-Smith (2009, 2011, 2012) and Skillings (2016) note that plants and animals horizontally acquire many of the microbes that make up their holobiomes, and they argue that holobionts are therefore not evolutionary individuals, because they do not generate parent-offspring lineages. On this latter view, symbiotic collectives function as evolutionary individuals only in case their symbionts reproduce together as a unit, as when some insects vertically transmit their obligate commensal bacteria. Sterelny (2011) counters that vertical transmission of symbionts is not necessary for a holobiont to function as an evolutionary individual, because symbiotic collectives are *interactors* (Hull 1980), the individual bearers of adaptations, regardless of whether their components reproduce together or propagate independently. In a voice resonate with Hull and Sterelny, Doolittle and Booth (2017) suggest that it is the symbiotic function itself, “the song not the singers”, which grounds the evolutionary individuality of a holobiont. The arguments presented in this article arise within the context of the holobiont debate, and will ultimately shed light on holobiontic individuality, but our proximate focus will be on a much simpler kind of symbiotic individual, one composed of a single multicellular plant and a single macrobial fungus.

The central thesis of this paper is that a *mycorrhizal collective*[[2]](#footnote-2), a biological individual composed of a plant together with a symbiotic fungus attached to its roots, is an evolutionary individual. Because mycorrhizal collectives overlap to form complex *mycorrhizal networks*, it follows that evolutionary individuals overlap. This matters for three reasons. The first is metaphysical. Metaphysicians should care about mycorrhizal individuality for the same kinds of reasons we care about the individuality of statues and clay – we want to know what there is in the world because such knowledge is valuable in itself. The second reason is ethical and practical. Some ethicists have argued that to be a thing of value at all, something must be an individual (Millstein 2019). If this reasoning is right, then environmental ethicists will want to know how floral communities arrange themselves into potential bearers of intrinsic value. More practically, conservationists need to know the difference between evolutionary individuals and mere groups of organisms in order to identify the objects of conservation and to assure their propagation into future generations. The third reason mycorrhizal individuality matters, and of primary interest for the present inquiry, are its implications for evolutionary theory and modeling, as mycorrhizal individuality entails not only overlapping evolutionary individuals but also a graded parameter of collective Darwinian individuality not included in current models.

 I open by noting some biological facts about mycorrhizal collectives which make them different from holobionts, and then I argue that *theoretical individuation* (Hull 1992, Pradeu 2012) must be employed to understand mycorrhizal individuality, as *phenomenal individuation* (Chauvier 2016) is not capable of revealing biological individuals in plants and fungi (Clarke 2012, Booth 2014b, Molter 2017). I next argue for a pluralism that recognizes multiple kinds of overlapping theoretically-defined individuals in multiply-decomposable biological systems (Wimsatt 2007, Haber 2012, 2016a). Employing theoretical individuation from this pluralistic perspective, I consider the functional roles which demarcate biological individuals according to two prominent versions, or models, of the theory of evolution by natural selection: David Hull’s (1980) *replicator/interactor* model and Peter Godfrey-Smith’s (2009) *Darwinian Populations* model. I show that mycorrhizal collectives function as individuals according to both versions of evolutionary theory. I conclude by arguing that it is the *potential* to reproduce collectively, not the state of having reproduced, which makes a symbiotic collective a Darwinian individual, and I suggest that this potential be understood in terms of the probability of symbiont lineages remaining together across reproductive events. In closing, I argue that the probability of vertical transmission constitutes a fourth parameter of collective Darwinian individuality, alongside Godfrey-Smith’s three parameters of *bottleneck*, *germ/soma* *separation*, and *overall* *integration* (2009, pg. 95).

**2.** **Why mycorrhizal collectives are not holobionts**

The *Mycorrhizae* (Gk. for “fungus root”) are a class of fungi who make their living by attaching themselves to the roots of plants, where they exchange minerals harvested from rocks and soil for carbohydrates produced in the plant’s leaves. Mycorrhizal fungi are mycelial, meaning they exist as interwoven networks of *hyphae* (pl. of *hypha*), elongated cell-like structures with openings at either end, which contain nuclei but allow cytoplasm and small organelles to flow freely into and out of the hypha. Structures composed of many interconnected hyphae, called *mycelia* (pl. of *mycelium*), can become quite large, perhaps exceeding in size even the largest plants and animals.[[3]](#footnote-3) Each mycelium is characterized by a common pool of cytoplasm that allows its nuclei, which can number in the trillions, to function as parts of a single physiologically integrated individual (Molter 2017).

Mycorrhizal fungi are classified into two broad categories; endomycorrhizal fungi form nutrient exchange structures inside the cell walls of their host plant, while ectomycorrhizal fungi accomplish nutrient exchange via structures that grow in between but do not penetrate the cells of the host[[4]](#footnote-4). The former include arbuscular mycorrhizal fungi, which engage in symbiosis with about 80% of vascular plant families but go largely unnoticed due to their fine threadlike structure and subterranean habitat (SchÜbler, Schwarzott, and Walker 2001). Ectomycorrhizal fungi are larger, and are found mostly in forests, where they serve as conduits through which trees share nutrients and immunological signaling molecules (Gorzelack et al 2015). Mycelial fungi are described in the literature variously as multicellular organisms and as singular massive multinucleate cells (Paoletti and Saupe 2009). Whether one considers a mycelium to be multicellular, unicellular, or something altogether different, mycorrhizal fungi should not be considered parts of their host plant’s holobiome, because they are macrobes in their own right.

The macrobial nature of a mycelium is more readily evident in ectomycorrhizal fungi, which produce large above-ground fruiting bodies, including familiar mushrooms such as porcinis and chanterelles. Endomycorrhizal fungi, on the other hand, are physically less substantial, and are sometimes considered to be part of the host plant’s holobiome (Hassani and Hacquard 2018); this is problematic for two reasons. While endomycorrhizal mycelia are often too thin to be seen with the naked eye, and thus might be considered microscopic, they are nonetheless long enough to connect the roots of multiple plants, and thus form physiologically integrated networks similar to those formed by ectomycorrhizal fungi (Song et al 2010). If we consider an endomycorrhizal mycelium to be a microbial part of a plant holobiont, then in the case of mycorrhizal networks we will be forced to countenance inches-long microbes, which are simultaneously parts of multiple holobionts. This would entail overlapping holobionts and would therefore violate Bordenstein’s and Theis’s (2015) seventh principle of holobionts. Secondly, endomycorrhizal mycelia have their own complements of symbiotic bacteria (Lastovetsky et al 2018), so each mycelium plays the role of a macrobe which anchors the identity of its own holobiont. To remain consistent with Bordenstein’s and Theis’s ten principles of holobionts, and to avoid the uneasy dyad, if not contradiction, of asserting that a single mycelium is both a microbe and a macrobe, it is better to drop the notion of mycelia as microbes altogether, and to recognize that endomycorrhizal collectives, like their ectomycorrhizal counterparts, are mutualistic associations composed of two macrobes.

 Holobionts, such as those which constitute human organisms, have naturally attracted the attention of philosophers and biologists, but they are incredibly complex, often containing trillions of individuals of thousands of different species (Qin et al 2010), and are therefore difficult to represent in evolutionary theoretic models. Mycorrhizal collectives, on the other hand, contain only two symbionts, and thus provide tractable case studies for modeling symbiotic evolutionary individuality. If we want to understand how symbiotic genomes encode adaptive phenotypic traits and how cohesion of symbiotic lineages across generations affects evolutionary individuality, then it makes sense to analyze the simplest cases first, and then apply the lessons learned to more complex symbiotic collectives such as ourselves. In sections four and five below, I argue that mycorrhizal collectives function both as interactors (Hull 1980) and as Darwinian individuals (Godfrey-Smith 2009), but before making those arguments, I defend the method of theoretical individuation which grounds both kinds of evolutionary individuality.

**3. Theoretical Individuation and Multiple Decomposability**

If a conservation biologist wanted to know how many bison there are in a given location, she would merely have to count them, as bison are the kind of thing that can be *phenomenally individuated*. To use the language of Stéphane Chauvier (2016), when we observe large familiar animals such as bison, our minds automatically generate *logico-cognitive individuals* that map onto *ontological individuals* in the world. Phenomenal individuation is less reliable at matching logico-cognitive individuals to ontological individuals when we observe plants and fungi. A tree, for example, might appear to be a single biological individual, even though mutations occurring during mitosis have made it a mosaic of genetically distinct cell lineages. When mosaicism results in differential fitness between cell lineages, the branches of a single phenomenal tree can function as distinct evolutionary individuals (Clarke 2012). On the other hand, a patch of mushrooms might appear to be a population of many individuals, when the mushrooms are in fact genetically identical parts of a single underground mycelium that functions as one evolutionary individual (Booth 2014b, Molter 2017). In the case of the tree, phenomenal individuation produces fewer individuals in the mind than there are in the world, and in the case of the mushrooms it produces more. Given the mismatch that arises between logico-cognitive and ontological individuals when we attempt to phenomenally individuate plants and fungi, if we hope to understand individuality in symbiotic collectives composed of plants and fungi, we will have to employ a more generally reliable method of individuation.

David Hull (1992) argues that in order to demarcate biological individuals, we must look beyond phenomena and note the functional roles played at various levels of organization, as those roles are defined in biological theory. Hull considers the theory of evolution by natural selection to be the only biological theory capable of providing a criterion of individuation, and he equates being an individual with being a unit of selection. In an earlier paper (1976), Hull notes three distinct kinds of evolutionary individuals: *units of mutation* (things that mutate), *units of selection* (things that are selected), and *units of evolution* (things that evolve). In yet another paper (1980), Hull further distinguishes between two kinds of units of selection: *replicators* and *interactors*. Replicators are units of selection that make copies of themselves, while interactors are units of selection that interact with the environment in ways that promote replication of their contained replicators. Evolutionary theory thus divides the biological milieu into four kinds of functional individuals for Hull: units of mutation, units of evolution, replicators, and interactors[[5]](#footnote-5).

Other authors give different accounts of evolutionary individuality. Richard Lewontin (1970), for example, identifies units of selection with reproducing members of evolving populations, a view adopted and modified by Peter Godfrey-Smith in his (2009) account of Darwinian individuality. Many biological individuals function both as interactors and Darwinian individuals, but these two functional roles do not always coincide in the same bit of living matter. For example, when the “zombie ant fungus” *Ophiocordyceps unilateralis* secretes metabolites that alter gene expression in its host, the “host behavior is an extended phenotype of the parasite’s genes being expressed through the body of an animal” (Fredericksen et al 2017). The body of an *Ophiocordyceps*-infected ant therefore functions as an interactor for fungal genes but is not part of the *Ophiocordyceps* Darwinian individual. What counts as an evolutionary individual thus turns both on the functional role an organized bit of living matter plays, and on the functional roles posited by the version of evolutionary theory employed for purposes of individuation. Different versions of evolutionary theory countenance different functional roles, and hence different individuals.

More recent work on theoretical individuation has focused on functional roles described in physiological theory. Thomas Pradeu (2012), for example, argues that immunity, as described in his *continuity theory of immunity*, provides a physiological criterion of individuation for organisms. An immune system polices what is and is not included in a physiologically integrated organism, so immunity demarcates the boundaries of these paradigm biological individuals. Pradeu (2012) suggests that his theory of immunity is the only physiological theory sufficiently developed to provide a reliable criterion of individuation. In a later work, Pradeu (2016) points to physiological individuation in domains such as neurology and development, which are not characterized by well-developed theories, as evidence that scientific individuation is not exhausted in theoretical individuation. Contrary to Pradeu, I take these additional kinds of physiological integration as providing theoretical criteria for individuation, under the broad umbrella of ‘theoretical individuation’, even in absence of well-developed theories describing them. There might be no rigorously articulated universal theory of metabolism or neurology, but there are models which describe metabolic and neurological integration at the local level; these local models can be understood as parts of theories (Geiri 2004, Wimsatt 2007). Every biological model comes with an implicit theoretical claim that the model is, in some relevant way, similar to the system modeled. It follows that theoretical individuation can be employed to demarcate individuals according to their functional role within a system, even when the ‘theories’ describing those systems consist of incomplete sets of local models. Theoretical individuation can thus be employed to identify metabolic individuals, neurological individuals, developmental individuals, immunological individuals, and perhaps other kinds of physiological individuals, along with the various kinds of evolutionary individuals identified by Lewontin, Hull, Godfrey-Smith, and other evolutionary theorists.

In many familiar examples of biological individuals, the various kinds of physiological integration coincide in a single discrete animal, which also functions as a unit of selection. This coincidence of functional roles in a single bit of living matter can make the question of biological individuality seem simpler than it really is, leading to the now obsolete idea that organisms are the only biological individuals (Pradeu 2016). If we look beyond large familiar animals, however, the various kinds of physiological integration often become disentangled from each other and detached from evolutionary role, as Janzen (1977) shows with dandelions and aphids.

Even in familiar megafauna such as bison, biological theories can carve nature in complex and incongruent ways. Hull (1976) notes that selection can occur at multiple levels of organization, including genes, cells, organisms, and groups of organisms (pg. 182), such that a species is divided into individual units of selection at each of these levels simultaneously. Metabolic and developmental theories, on the other hand, individuate particular animals, while immunological theories describe functional units both at the level of particular bison, and, to a lesser degree, at the level of the entire herd (Fine 1993). Biological theories thus carve the species *Bison bison* into multiple discordant sets of individuals, a condition Bill Wimsatt (2007) calls *multiple decomposability.* Different biological theories divide a given system into different sets of individual parts, according to the roles those parts play in theory, and insofar as multiple theories accurately illuminate functional divisions within the system, no one theoretical decomposition is ontologically privileged over the others.

The upshot, for the purpose of this essay, is that biological individuality is complex, diverse, and multiply realizable. Not only must we recognize multiple kinds of biological individuals, we must also be aware that the various kinds of individuals can have nested and overlapping boundaries. Demonstrating that a mycorrhizal collective functions as a metabolic or an immunological individual, for example, does not prove that it also functions as an evolutionary individual, as these various functional roles can come apart. Nor does it follow that because a plant or a fungus is an evolutionary individual in its own right that a symbiotic collective composed of a plant and a fungus is therefore *not* an evolutionary individual, as evolutionary individuality can occur at more than one level in a multiply decomposable system. The only thing required to demonstrate evolutionary individuality in a mycorrhizal collective is to show that it plays the functional role of an individual according to evolutionary theory; that is what I aim to show in the next two sections.

**4. Mycorrhizal Collectives as Interactors**

David Hull (1976) employs evolutionary theory to decompose the living world first into species, referring to species as “chunks of the genealogical nexus” (pg. 174). Hull makes this first cut at the level of species, instead of at kingdoms or supraspecific phyla, on grounds that, according to evolutionary theory, species are the things that evolve. Quoting Ernst Mayr Hull says, “Species are the real units of evolution, they are the entities which specialize, which become adapted, or which shift their adaptation” (Mayr 1969; in Hull 1976, 183). Hull next decomposes species into organisms, rather than into varieties or local populations, on grounds that organisms are the things selected in natural selection; “the organism is *the* unit of selection” (pg. 181). Hull then decomposes organisms into their spatiotemporal parts, some of which function in a third evolutionary role; “the gene is *the* unit of mutation” (Pg. 181). At each level of decomposition, Hull carves the genealogical nexus into parts according to the roles those parts play in evolutionary theory. In this highly abstract and simplified sketch of evolution by natural selection, a symbiotic collective does not function as an evolutionary individual, because it is neither an evolving species, nor a selectable organism in an evolving species, nor a mutable part of a selectable organism.

Hull acknowledges, however, that evolutionary reality is far more complex than what he describes in the simplified model.

Most biologists see the evolutionary process as being much more complicated than this. Genetic changes can be as slight as the alteration of a single nucleotide or as major as the loss or gain of entire chromosomes. As Lewontin (1970) has argued, selection occurs at an even wider range of levels of organization, from macromolecules to kinship groups, probably at the level of populations, possibly even at the level of species. There is no doubt that entities such as genes, gametes, organisms, and certain kinship groups possess the degree and kind of organization necessary to function as units of selection… Like mutation and selection, evolution occurs at more than one level of organization. At the very least, populations and species evolve (Hull 1976, pg. 182).

Is it possible that a symbiotic collective might function as a unit of selection, and hence be an evolutionary individual, according to a model of evolution that reflects the genuine complexity of nature? Hull does not say, but what’s clear from his account is that individuality tracks evolutionary role, and the three functional roles posited in his version of evolutionary theory operate at multiple levels of organization up and down the biological hierarchy. Given the complexity and multiple decomposability that follows from Hull’s (1976) account of evolutionary individuality, a mycorrhizal collective might play a functional role as an evolutionary individual, alongside the evolutionary roles played by its component symbionts, provided that it is organized in such a way that it can be selected under a regime of natural selection.

In a later paper (1980), Hull recognizes two distinct ways an individual might be selected, the second of which I now argue includes mycorrhizal collectives as units of selection. Hull divides units of selection into *replicators* and *interactors*. Replicators include genes, chromosomes, asexual microbes, and any other biological individual that forms lineages by making more or less exact copies of itself. *Interactors*, on the other hand, include organisms and other biological individuals that encapsulate replicators, exhibit adaptive traits, and interact with the environment in ways that promote replication of their contained replicators. Genes are the paradigm replicators, while organisms are the paradigm interactors.

When an organism’s genome encodes phenotypic traits that are well adapted to its environment, the organism will interact with the environment in ways that promote the replication of its genes, both by growing and by reproducing. An organism thus functions as a unit of selection, insofar as nature “selects” the best adapted organisms for reproduction and the least adapted for elimination from the reproductive contest. Genes, on the other hand, function as units of selection insofar as differential reproduction or elimination at the organism level causes copies of an organism’s genes to become more or less abundant in subsequent generations. While gene replication is necessary for organism reproduction, and ultimately vice versa, the two processes are nevertheless theoretically distinct. Key to the distinction between replicators and interactors, and to understanding why symbiotic collectives can function in the latter role, is that replicators hold no adaptations beyond the ability to replicate – their fitness derives from their ability to construct traits that are adaptive at the level of the interactor, and, crucially, adaptive phenotypic traits don’t arise from single genes, but rather from combinations of genes operating as parts of a genome[[6]](#footnote-6).

 That adaptive traits arise from genomes, not from genes in isolation, is key to Mindell’s (1992) argument that holobionts are evolutionary individuals; it is the *hologenome*, Mindell says, not merely the genome of the macrobe, which drives the development of adaptive traits in a holobiont. The same is true for mycorrhizal collectives, in which plant genes and fungal genes combine to form a functional symbiotic genome that encodes adaptive phenotypic traits. Most notable among these symbiotically constructed adaptations is the nutrient exchange interface, which develops from a complex process in which molecules produced by the fungus activate plant genes and vice versa (Handa et al 2015). Other adaptive traits which reside in a mycorrhizal collective include pathogen resistance (Cameron et al 2013) and the efficiency with which a mycorrhizal collective utilizes available resources (Augé 2001).

In order to function as a replicator, an individual such as a chromosome or a microbe must pass along all its genes when it makes copies of itself, but the evolutionary individuality of aninteractor does not turn on its encapsulated replicators propagating together as a unit. When a sexual organism (a paradigm interactor) reproduces, it passes on to its offspring only some of its genes, even though its fitness for reproduction derives from the interaction of all its genes. It follows that an interactor’s adaptive traits can promote independent replication of its contained replicators. Because a mycorrhizal collective’s symbiotically constructed adaptive traits promote the replication of both plant and fungal genes, the mycorrhizal collective functions as an interactor, and hence as an evolutionary individual, regardless of whether the plant and the fungus reproduce together or independently.

**5. Mycorrhizal Collectives as Darwinian Individuals**

Godfrey-Smith’s (2009) *Darwinian Populations* model of evolution by natural selection requires that units of selection be reproducing members of populations, as reproduction is the way a unit of selection transmits its fitness affecting traits to individuals in the next generation (Lewontin 1970). Concerning the Darwinian individuality of symbiotic collectives, Godfrey-Smith compares aphids colonized by vertically transmitted microbial symbionts (aphid-buchnera collectives) to squid colonized by horizontally acquired microbial symbionts (squid-vibrio collectives), and he argues that only the former function as Darwinian individuals. When component symbionts reproduce together as a unit, as in the case of an aphid-buchnera collective, symbiotic collectives in successive generations “stand in parent-offspring relations to each other”, a condition Godfrey-Smith counts as necessary for Darwinian individuality (2012, pg. 30). An aphid’s symbiotic microbes are bundled into gametes and transferred from parent to offspring, so there is a single line of descent connecting an aphid-buchnera collective in one generation to an aphid-buchnera collective in the next generation. Squid, on the other hand, acquire their symbiotic microbes from the sea rather than from their parents, so there is no unitary line of descent connecting a squid-vibrio collective in one generation to a squid-vibrio collective in a subsequent generation, and hence no transmission of adaptive symbiotic gene combinations. Whereas the lineages of partner symbionts remain bundled through a reproductive bottleneck in the case of aphid-buchnera collectives, the lineages of component symbionts come apart at reproduction in the case of squid-vibrio collectives, so only the former are reproducers in the sense Godfrey-Smith counts as necessary for Darwinian individuality.

 Mycorrhizal collectives appear to meet Godfrey-Smith’s conditions for being reproducers, in at least some circumstances, as the lineages of both fungal and plant symbionts often remain bundled through reproduction. *Pseudo-vertical transmission* (Wilkinson 1997), which occurs when a seedling sprouts in soil occupied by its parent’s mycorrhizal fungus and subsequently forms a mycorrhizal symbiosis with the same fungus as the parent, generates a line of descent between progenitor and progeny at the level of the mycorrhizal collective, and it enables the inheritance of symbiotic gene combinations, along with the adaptive traits those combinations encode. Because pseudo-vertical transmission preserves adaptive gene combinations in successive stages of a hereditary lineage, it accomplishes the same evolutionary work as conventional vertical transmission, so whenever a mycorrhizal collective reproduces with pseudo-vertical transmission, it functions as an evolutionary individual in the same way an aphid-buchnera collective does.

 In cases where a plant and its mycorrhizal fungus reproduce independently and find new symbiotic partners in the next generation, a mycorrhizal collective does not meet Godfrey-Smith’s condition for Darwinian individuality, but every mycorrhizal collective nonetheless has the *potential* to engage in pseudo-vertical transmission. The potential to pass along its adaptive symbiotic genome intact seems to be sufficient to make a mycorrhizal collective function as a selectable Darwinian individual, even if it has not yet actually reproduced in this way. Indeed, it would be odd to think that something becomes a Darwinian individual only after it reproduces, as requiring actual reproduction would exclude from the class of Darwinian individuals juvenile members of paradigm Darwinian populations, as well as every individual selected for elimination without reproducing. To be a unit of selection is to be a contender in the struggle for existence, not necessarily to be a winner of the contest. When Darwinian individuality is understood in terms of the potential to reproduce, every mycorrhizal collective counts as a Darwinian individual, because every mycorrhizal collective has the potential to pass on to the next generation, via pseudo-vertical transmission, its adaptive symbiotic genome[[7]](#footnote-7).

**6. Collective Reproduction and the Great Tesseract of Being**

 While the Darwinian individuality of a symbiotic collective follows from its potential to reproduce with vertical or pseudo-vertical transmission, like other properties which affect Darwinian individuality, the potential to vertically transmit comes in degrees. Godfrey-Smith (2009) describes a scale of Darwinian individuality in collective reproducers, which includes three graded parameters: bottleneck, germ/soma separation, and overall integration. Biological entities which score high on this scale are Darwinian individuals to a high degree, while biological entities which score low on all three parameters are only marginally Darwinian. The 3D model of this scale (pg. 95), which Ken Waters (2018) refers to as “The Great Cube of Being”, features animals like “Us” at its apex, while plants and slime molds appear further back and down, as the latter score lower on the three graded parameters. While Godfrey-Smith argues there is no absolute bottom to this scale (marginal Darwinian-individuality grades smoothly into non-Darwinian-individuality), his discussion of symbiotic collectives nonetheless implies that making it onto the scale at all is a binary condition; vertical transmitters such as aphid-buchnera collectives are Darwinian individuals, while non-vertical transmitters such as squid-vibrio collectives are not. Pseudo-vertical transmission in mycorrhizal collectives, however, fills in that gap, showing that there are gradations between these two extremes.

*Coccoloba uvifera*, the seagrape, a tree native to Caribbean coastal beaches, engages in mycorrhizal symbiosis predominately with earth-ball fungi of the genus *Scleroderma*, which help the seagrape tolerate salt (Bandou et al 2006). Seagrapes were introduced throughout the tropics in the 20th century, and their mycorrhizal partners have followed them, due to a high degree of pseudo-vertical transmission (Séne et al 2018). Seagrape fruits have a tendency to aggregate *Scleroderma* spores as both are lying on the beach, so when waves or animals move clusters of fallen seagrapes to new locations, *Scleroderma* spores adhering to the fruits are transported with them and colonize new seedlings as soon as they sprout. The seagrape-scleroderma collective’s traits of salt tolerance and co-dispersal of propagules evolved from a history of pseudo-vertical transmission, and these traits make it likely that pseudo-vertical transmission will continue into the future. While the probability of seagrape and *Scleroderma* lineages remaining paired across reproductive events is high, this probability in less than one, as the mechanism of dispersal does not guarantee vertical transmission, and because both the plant and the fungus are capable of pairing with other partners (Bandou et al 2006). It follows that seagrape-scleroderma collectives fall just below aphid-buchnera collectives on a gradient of vertical transmission.

This gradient, which I’ll label *P(V*) for the probability of vertical transmission[[8]](#footnote-8), is correlated with host-symbiont specificity. Seagrapes largely specialize in *Scleroderma*, and this increases the P(V) of seagrape-scleroderma collectives, because it limits the availability of spores from other mycorrhizal fungi in the vicinity of seagrape seeds. Mycorrhizal collectives composed of generalists, on the other hand, have a lower P(V). Generalists such as oaks and pines form mycorrhizal symbioses with hundreds of species of mushrooms, and single trees frequently host multiple fungal species simultaneously. An oak colonized by both a chanterelle mycelium and a porcini mycelium, for example, has the potential to vertically transmit with either of its symbionts, and when understood as a probability, this potential is divided between them, as a seedling might be colonized by either the chanterelle or the porcini, depending on which side of the tree the acorn falls.[[9]](#footnote-9)

Other factors that affect P(V) include the morphology of seeds and local ecological conditions. Heavy seeds such as acorns and walnuts have a higher probability of falling close to the parent tree, and hence a higher probability of pseudo-vertical transmission, than do the seeds of trees such as maples and birch, which are lighter and have evolved ‘wings’ for long distance wind dispersal. Microhabitats, such as wet places in otherwise xeric environments, seem especially well suited for promoting pseudo-vertical transmission. Birch Spring in the Henry Mountains of southern Utah, for example, produces a trickle of water that flows for about ten meters before drying up, and thus produces a tiny riparian habitat that hosts a handful of birch trees colonized by mycorrhizal fungi of the genus *Cortinarius* (Molter 2018). Birch seeds and *Cortinarius* spores are both capable of long-distance wind dispersal, so the decedents of both symbionts have the potential to find new mycorrhizal partners at other springs in the Henry Mountains, but the vast majority of seeds and spores fall either into the surrounding scrubland where they perish or into the few square meters of moist soil around Birch Spring. Consequently, a mycorrhizal collective living at this tiny oasis is more likely to engage in pseudo-vertical transmission than one composed of the same species living in a larger riparian habitat, such as the bank of a river. Another important local condition that affects P(V) is the age and density of a forest. In mature forests, where seedlings must grow up in the shade of their parents, mother trees feed baby trees by sending nutrients through a connecting mycorrhizal fungus (Gorzelak et al 2015); such parental support is available only in case of reproduction with pseudo-vertical transmission.

These examples show that the potential to reproduce with vertical transmission is not a bivalent condition, but instead grades up or down depending on a variety of evolved and local environmental factors. I suggest here that P(V) be understood as a fourth parameter of graded Darwinian individuality, alongside the three parameters included in Godfrey-Smith’s scale of collective reproducers. Like the other three parameters, P(V) should be understood as grading asymptotically towards the upper and lower limits of the spectrum. Even in squid-vibrio collectives, the paradigm non-Darwinian individuals, there is some non-zero probability that, by pure chance, the descendants of a squid’s symbiotic bacteria will end up in the light organ of the squid’s offspring. This probability is very low, and such collective reproductive events are so rare that they have very little impact on the evolution of squid and *Vibrio*, but the probability is not zero. Similarly, there is some non-zero probability, or at least the biological possibility, that an aphid could fail to vertically transmit its endosymbiotic bacteria. This latter probability is extremely low indeed, as aphids are dependent on *Buchnera* for the synthesis of essential amino acids not present in their food, but it’s not hard to imagine potential scenarios in which a population of aphids finds a richer food source or acquires an alternate species of commensal bacteria that performs the same essential function as *Buchnera*. Both hypothetical scenarios would render the vertical transmission of *Buchnera* non-necessary for aphid reproduction, and because both scenarios are possible, the probability of aphid and *Buchnera* lineages remaining entwined through reproduction is slightly less than one. While the P(V) of squid-vibrio collectives approaches zero and the P(V) of aphid-buchnera collectives approaches one, neither kind of symbiotic collective should be thought of as categorically lineage-generating or categorically non-lineage generating, but rather as occupying the top and the bottom regions on a graded scale of potential lineage-generators.

 By adding P(V) as a fourth graded parameter of Darwinian individuality in collective reproducers, we transform Godfrey-Smith’s “Great Cube of Being” into a hypercube or tesseract. The width of a biological entity’s reproductive bottleneck, the degree to which its germline cells sequester themselves from those that develop into an interactor, the entity’s overall physiological integration, and, the probability of its component lineages remaining together in future generations, all coincide to resolve a biological entity’s degree of Darwinian individuality. The Great Tesseract of Being is, of course, an abstract model, which only partially represents processes which sort the biological milieu into individuals. There are likely other parameters of collective Darwinian individuality which could add further dimensions to the model, but it’s interesting to see at the apex of this 4D scale not a holobiont like “Us”, but instead a collectively propagating bundle of insect and bacterial lineages.

**7. Conclusion**

 The arguments presented here show that mycorrhizal collectives function as evolutionary individuals, both in the sense of Hull’s interactors, and in the sense of Godfrey-Smith’s Darwinian individuals. I have further argued that the probability of vertical transmission constitutes a fourth parameter of graded Darwinian individuality. I have not, however, attempted to evaluate these two versions of evolutionary theory. The question of which is the correct or most representative evolutionary-theoretic model has been avoided, because I think both descriptions of natural selection have merit. If we embrace a pluralism about natural selection, and hold that both Hull’s and Godfrey-Smith’s models represent, in some relevant way, real evolutionary processes, then functioning as an individual according to both models might indicate that symbiotic collectives with high P(V) are more robustly individual than those which function as interactors but rarely vertically transmit.

I have left for future work the question of individuality in complex mycorrhizal networks, but in showing that each plant-fungus pair functions as an evolutionary individual, I have indirectly shown that mycorrhizal networks are constituted by overlapping multispecies individuals. It’s intriguing to ponder whether mycorrhizal individuality might be transitive, such that all the plants and fungi in a mycorrhizal network constitute parts of a massively multispecies evolutionary individual, but such higher order symbiotic individuality would be complicated by reproductive competition between constituents of the network. Sorting out evolutionary individuality in complex symbiotic systems such as forests or human holobionts will no doubt prove more difficult than what we’ve seen in the simple case of two symbiotic macrobes, but understanding that each pair of symbionts constitutes a unique evolutionary individual is the first step.

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1. According to the seventh principle of holobionts (Bordenstein and Theis 2015), each holobiont necessarily contains a single macrobe, which grounds the identity of the holobiont as its microbial complement changes over time. [↑](#footnote-ref-1)
2. I use the term “mycorrhizal collective” to refer to the symbiotic association of one plant and one fungus, and the term “mycorrhizal network” to refer to more complex associations of plants and fungi which occur when a mycelium connects the roots of multiple plants. Most mycorrhizal collectives in nature occur as parts of mycorrhizal networks. [↑](#footnote-ref-2)
3. A single genet of the honey mushroom *Armillaria solidipes* covers 3.7 square miles and is claimed by some to be the world’s largest organism (Schmitt & Tatum 2008), though no tests have been conducted to determine if “The Humongous Fungus” remains connected as a single mycelium, or if it has become fragmented over its 8000 year life. [↑](#footnote-ref-3)
4. I use the term “category” to indicate that endo and ecto mycorrhizal fungi do not map onto distinct clades, but rather denote physiological modes of symbiotic interaction. Ectomycorrhizal fungi are very diverse and do not form a single monophyletic group. Endomycorhizal fungi are likewise diverse, consisting of several distinct phyla, including: arbuscular mycorrhizae, ericoid mycorrhizae, orchid mycorrhizae, and monotropoid mycorrhizae (Peterson et al 2004). [↑](#footnote-ref-4)
5. Doolittle and Booth (2017) extend Hull’s arguments for functional individuality beyond biological entities that perform the function, arguing that it is the biological function of microbial communities itself (metabolite synthesis for example) that is the target or object of natural selection, rather than the entities which perform the function – it’s the song not the singers! Interestingly, on this view, natural selection modifies lineages of microbial activities rather than lineages of microbes. Just as a song can be sung and modified by more than one band, evolving lineages of microbial activities (songs) need not map onto lineages of replicating microbes. For Hull (1980), the selection of a functional role is selection on the entity performing that role, so selection and evolution remain tied to phylogeny in Hull’s functional account of evolutionary individuality. [↑](#footnote-ref-5)
6. Hull says “The only adaptations they [replicators] need to exhibit are those to promote replication” (1980 pg. 318). All other adaptations arise, according to Hull, at the level of the interactor. Hull notes that a single biological individual can function simultaneously as a replicator and an interactor, as in the case of asexual microbes. I’m grateful to a referee for pointing out that some genes, like asexual microbes, might function in both roles simultaneously. Miotic drive genes, for example, seem like good candidates for gene-level interactors. [↑](#footnote-ref-6)
7. Mycorrhizal symbiosis ranges from parasitic to mutualistic, depending on a number of factors, including the species of plants and fungi involved. Endomycorrhizal symbiosis tends toward mutualistic, while ectomycorrhizal symbiosis can be either mutualistic or parasitic, often depending on local ecological conditions. Yellow morels, for example, form mutualistic symbioses with elm trees, but are thought to become parasitic and contribute the death of host trees that contract Dutch elm disease (Arora 1986). My arguments here focus on the maintenance and evolution of adaptive (mutualistic) symbiotically-constructed traits, though pseudo-vertical transmission in maladaptive pairings might play a role in evolving such combinations from parasitic toward mutualistic. [↑](#footnote-ref-7)
8. I include under P(V) a symbiotic collective’s probability of reproducing either with vertical transmission or pseudo-vertical transmission. Traditional vertical transmission might be understood as cases in which P(V) equals or approaches 1, while pseudo-vertical transmission can be thought of as cases where P(V) < 1. While I will not here defend a theory of probability, I think P(V) can be best understood as a frequency when looking backward on the history of evolution, and as a propensity when looking forward. [↑](#footnote-ref-8)
9. Varying degrees of pseudo-vertical transmission can be found in biological contexts beyond mycorrhizal collectives. Pedroso (2019), for example, notes that some species of microbes in a biofilm (a physiologically integrated assemblage of numerous microbial species) tend to stick together and co-disperse to found new colonies when a biofilm is broken apart by weather or other natural phenomena, while other component species in a biofilm have a low probability of co-dispersal. Attending to the varying P(V)s of their components might shed light on the question of selection and individuality in biofilms (Clarke 2016, Pedroso 2017). [↑](#footnote-ref-9)