Getting at the basics of multicellularity

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Abstract

This chapter asks three basic questions about multicellularity: What is multicellularity? How is it explained? How is it valued? Because such a large range of phenomena are labelled as ‘multicellular’, it is unlikely there will be a single explanation of why multicellularity has evolved and persisted in some lineages. Standard reasons for emphasizing the importance of the evolution of multicellularity apply equally to unicellular lifeforms.

## 2.1 Introduction

All scientific investigations are underpinned by basic assumptions, and the study of multicellularity is no exception. Asking questions about these foundations can help illuminate the field's subject matter and investigative tools. This chapter addresses three general questions about multicellularity:

1. What is multicellularity?
2. How is multicellularity explained?
3. How is multicellularity valued?

Multicellularity is a broad label that covers an important attribute of living systems. However, because multiple phenomena are covered by the term multicellularity, any simple categorization scheme is likely to fail to capture how multicellularity manifests across the tree of life.

Taking the various dimensions of multicellularity into account has implications for how multicellularity is theorized and explained. In particular, a single overarching evolutionary explanation of multicellularity as an adaptive phenomenon might in certain respects be inadequate and misleading. A whole range of different, highly tailored explanations might be more appropriate for the multiple versions of multicellularity on the evolutionary record.

Tangled up with both these issues of categorizing and explaining multicellularity is another very basic one to do with how multicellularity is valued. This chapter asks whether multicellularity is any 'better' than unicellularity in any evolutionary or ecological sense.

## 2.2 Categorizing multicellularity

> 'Like the attempt to define "life", defining multicellularity is a tenuous endeavor, often clouded by anthropocentrism' (Lyons and Kolter 2015, p. 21)

The diversity of origins and forms of multicellularity across the domains of life is well-recognized (e.g., Parfrey and Lahr 2013). Multicellularity is often characterized as a 'repeated invention' and thus an instance of convergent evolution (Rokas 2008, p. 472; Szathmáry 2015). However, there are numerous cross-cutting distinctions made about multicellularity that show it to be a multi-faceted phenomenon: clonal versus aggregative, simple versus complex, obligate versus facultative, environmentally versus internally driven.

### 2.2.1 Clonal versus aggregative multicellularity

A fundamental way of categorizing extant multicellularity is to divide it into 'aggregative' and 'clonal' forms (e.g., Grosberg and Strathmann 2007). The former reproduce separately but cluster together by various means; the latter arise from a series of dividing cells that remain closely connected and may differentiate into further cell types after additional division.

Clonal multicellularity is well-known in animals, plants, algae and fungi, but it also occurs in microbes, which are normally defined as unicellular. Cyanobacteria form filaments, some with differentiated cell types, by not separating completely after cell division (Schirrmeister et al. 2011; Claesson et al. 2014). *Streptomyces* and many other actinobacteria also form differentiated multicellular bodies, but via coenocytes that form hyphal networks and eventually culminate in spore production (Barka et al. 2016; Claesson et al. 2014). *Zoothamnium*, an aquatic ciliate, forms large branching colonies with a common stalk formed from a syncytial fusion of cells (Clamp and Williams 2006). Some amoeboid organisms also use coenocytic and syncytial multicellular structures from which they eventually release

amoebal progeny (e.g., *Ichthyosporea*, *Syssomonas*). And although magnetotactic bacteria are usually referred to as 'aggregates', some of them undergo synchronized cloning to replicate as hollow spherical assemblies (Abreu et al. 2014), as do their non-magnetotactic multicellular relatives (LeFèvre et al. 2010).

Aggregative forms of multicellularity with cell differentiation are seen in the fruiting body phenotypes of organisms such *Dictyostelium*, the ciliate *Sorogena*, and a number of other eukaryotic groups (Schilde and Schaap 2013; Kaiser 2003; Brown et al. 2012). Many aggregatively multicellular eukaryotes do not carry out everyday activities of feeding and movement in their differentiated multicellular states, which are primarily formations for collective spore dispersal (Cavalier-Smith 2017). In Bacteria, myxobacteria and *Bacillus subtilis* are the classic exemplars of multicellularity (Kroos 2007). Other bacterial taxa also form multicellular structures by aggregative means (e.g., *Salmonella*, *Escherichia coli, Proteus mirabilis*) and some of them feature differentiation in cell types (e.g., *Pseudomonas aeruginosa*). In Archaea, several methanogens form tight aggregations, in which unicellular dispersals lead to new aggregative formations (Robinson et al. 1985; Kern et al. 2015). The lifecycles of these apparently obligatory aggregations dictate individual cellular morphologies.

### 2.2.2 Complex versus simple multicellularity

Another way of distinguishing forms of multicellularity is to place each instance of it on a gradient of complexity. This is often estimated by numbers of cell types (e.g., Rokas 2008; Knoll 2011; Bonner 2004). Particular versions of more differentiated multicellularity sometimes accomplish 'three-dimensional' organization (e.g., Nagy, Kovács and Krizsán 2018), which is a property mostly attributed to animals, plants and fungi. On this spectrum of simple-to-complex multicellularity, bacterial and archaeal multicellularity is not that different from 'simple' eukaryotic multicellularity. These less differentiated multicellularities are considered to be much more limited in evolutionary and phenotypic innovation than the 'complex multicellularity' exhibited by plants, algae, animals and fungi (e.g., Knoll 2011).

Is thinking of complexity in this way helpful? Attempts to quantify complexity levels mostly map on to organisms already believed to be complex (Bell and Mooers 1997; Cock and Collén 2015). Such quantifications sideline the immensely complicated lifecycles that many unicellular organisms with facultative multicellular stages undergo (Herron et al. 2013). But because complexity is often discussed with examples like animals in mind, the intricacies of lifecycles rarely count. Nor does metabolic complexity, which is at least as (if not more) likely to be found in less morphologically complex organisms (Poole et al. 2003). Other evaluations argue that due to the many steps and mechanisms involved (i.e., more complexity), 'aggregative multicellularity might be … more difficult to evolve', and yet, at the same time, these 'simple' aggregations might have 'more limited evolutionary potential' (Brunet and King 2017, pp. 127-128).

How is such limitation known? Again, largely by not measuring up to the morphological standards of animals and plants. And even then, some huge but unicellular algae (coenocytes) display great morphological complexity, developmental phases, and bodily regions (Mandoli 1998; Ranjan et al. 2015). It might seem even more remarkable to achieve these capacities with one – albeit large – cell than with numerous differentiated cells. If complexity were measured by lifecycle complexity or sheer numbers of reproductive strategies, many plants and fungi would score reasonably well (Herron et al. 2013; Tripp and Lendemer 2017; Naranjo-Ortiz and Gabaldón 2020), along with a huge range of unicellular organisms that only occasionally opt for multicellular states. Many animals would score very poorly on this

measure of complexity, which would mean equating all instances of clonal multicellularity with greater innovation might not be justifiable.

### 2.2.3 Obligate versus facultative multicellularity

A further distinction is that of obligate and facultative multicellularity: whether an organism (or offspring in a lifecycle) persists in a unicellular state or not. This dimension can cut across the clonal-aggregative divide. Although it is often thought that obligate multicellularity is always clonal (e.g., Fisher et al. 2013, p. 1120), and aggregative multicellularity is mostly facultative – in that it occurs in multigenerational life cycles of organisms that have unicellular stages (Brown et al. 2012) – this is not always the case. For instance, some aggregative multicellularity can occur entirely without a unicellular stage. Although multicellularity is almost always discussed in relation to single-species arrangements, lichen propagules – containing their photobiont – are an example of multispecies multicellular reproduction of obligate symbiotic aggregations (Tripp and Lendemer 2017). These lifelong commitments to multicellularity might be considered, therefore, exceptions to general observations that 'no multicellular organisms that develop by aggregation also produce multicellular propagules' (Grosberg and Strathmann 2007, p. 626).

And although a great deal of clonal multicellularity in large eukaryotes is obligatory, at least some forms of clonal multicellularity are facultative (e.g., choanoflagellates, plasmodial slime moulds). Moreover, some clonal organisms reproduce from multicellular propagules, meaning a multicellular organism gives rise to another multicellular organism (e.g., vegetatively propagating plants, modular clonal animals, mycelial fragmentation in fungi, choanoflagellate colonies and rosettes, experimental snowflake yeast). In other words, these multicellular entities need not have an obligatorily unicellular stage, which is often taken to be a hallmark of the clonal multicellularity they represent (e.g., Niklas and Newman 2013; Grosberg and Strathmann 1998).

Making the situation more complicated are multicellular magnetotactic bacteria that have unviable unicells and always reproduce as multicellular units. These organisms are thus the most obligatorily multicellular of all (Keim et al. 2004; Abreu et al. 2014). This strategy falls outside standard definitions of clonal multicellularity (serial cell division from a single cell progenitor). Moreover, recent analysis shows genetic variation between cells in the multicellular magnetotactic assemblage (Schaible 2020). The general lesson is that it is difficult to be too definitive about how obligatory or not any form of multicellularity will be, or even whether clonal multicellularity absolutely requires a unicellular bottleneck.

### 2.2.4. Environmentally versus internally triggered multicellularity

A final distinction is sometimes made between multicellularity that is triggered environmentally or by signals internal to the organism. Many facultatively multicellular organisms require some sort of environmental trigger to initiate the developmental programmes of aggregative and even clonal multicellularity. Dictyostelia are an example of the former, for which the classic trigger is starvation (Schilde and Schaap 2013), as are some algae, for which aggregative multicellularity may be invoked by the presence of predators (Kapsetaki and West 2019). Choanoflagellates can be an example of the latter, when bacterial signals trigger the serial cell divisions that result in multicellular development (Alegado et al. 2012). But obligate clonal multicellularity, especially the versions leading to many cell types and organs, appears to be driven internally even if environmental conditions affect aspects of the multicellularity that is attained (Fisher and Regenberg 2019).

Although internally triggered multicellularity is usually discussed in relation to plants and animals, some cyanobacteria that develop into clonal filaments do so without environmental

triggers (Herrero et al. 2016). Obligate multicellularity without a unicellular stage, as in magnetotactic bacteria, also appears to be internally driven rather than environmentally cued (Keim et al. 2004). But in important respects, this distinction is not very helpful. 'Internal' triggers originate from the cellular constituents of the developing organism, whereas external signals can come from other organisms in close proximity. In the latter case, such signals are what prompt aggregation and eventually the internalization of those very same signals. For example, when *Pseudomonas* aggregates begin the differentiation of cell structures (e.g., 'mushroom' formations), at least some of the signals to differentiate are at that point 'internal' to the developing multicellular organism (Klausen et al. 2003).

2.2.5 Summarizing multicellularity distinctions

Table 2.1 shows how three distinctions (clonal/aggregative, obligate/facultative, internal/environmental) produce eight loosely defined states of multicellularity. All of them have representatives in the living world today. Each cell in Table 2.1 is represented by an example discussed in the chapter. The table could be further complicated by adding a complex/simple distinction, but since this would involve judgements favouring either complex lifecycles or cell differentiation (see 1.2), or some other factor (McShea 1996), that dimension would not be informative without considerable qualification.

Table 2.1 Eight states of multicellularity

| | Facultative | Obligate | Internal trigger | Environmental cue |
|---|---|---|---|---|
| Clonal | Plasmodial slime moulds, streptomyces | Cyanobacteria | Metazoans | Choanoflagellates |
| Aggregative | *Dictyostelium* | Methanobacteria | *Pseudomonas* (mushroom structures) | Myxobacteria |

In addition to the cross-cutting nature of these distinctions, phylogenetic reconstructions make clear how many very different phenomena are lumped beneath the label of 'multicellularity', even in close evolutionary quarters (e.g., Brown et al. 2012; Sebé-Pedrós et al. 2017; Schirrmeister et al. 2011). And beyond the possible permutations of clonal, aggregative, facultative, obligatory, genetically driven and environmentally cued development lie a range of very different mechanisms and cellular behaviours. Incomplete separation, sticky adherence, coenocyte growth, coenocyte cellularization, syncytial fusion, and baroque lifecycles are just some of the phenomena that distinguish the varieties of multicellularity distributed across the tree of life. Talking about multicellularity in general and especially '*the* evolution of multicellularity' might be misleading, because it would obscure the different mechanisms and evolutionary histories of such multicellular states. The overall plurality of multicellular states has implications for how relevant phenomena are investigated.

2.3 Explaining the evolution of multicellularity

Researchers interested in multicellularity as a broad phenomenon study it not just to understand its various forms but also to gain insight into its evolution. Although these investigations explore a range of phenomena and use different methods, they address similarly basic questions.

2.3.1 Explaining convergence and divergence

The diversity of manifestations of multicellularity raises questions about the evolutionary relationships between different versions. Do certain forms give rise to others? Or are they separate evolutionary innovations sharing only some general selection pressures? Although aggregative multicellularity is often thought of as a bit of a dead end, in that it does not explore a great deal of phenotypic (i.e., morphological) space (e.g., Brunet and King 2017), clonal multicellularity is usually described as leading to extensive innovation and impressive morphological diversity (e.g., Szathmáry 2015). Does this mean that the mechanisms and selection pressures of clonal multicellularity are different from those of aggregative versions?

An example that sheds light on this question involves unicellular sister groups to metazoans and choanoflagellates (together forming the clade of Holozoa; see Figure 2.1). Members of these groups are thought to illuminate how metazoans originated and subsequently evolved. The closest group, filastereans, displays a sophisticated form of aggregative multicellularity and development (Sebé-Pedrós et al. 2013). Yet the next closest group, ichthyosporeans (the sister to animals, choanoflagellates and filastereans), deploys yet another means of reaching multicellularity, in that the multicellular form emerges from the cellularization of a coenocyte, with released cells heading off to found their own multicellular body (Suga and Ruiz-Trillo 2013; Sebé-Pedrós et al. 2017). These organisms are therefore clonally multicellular.

Choanoflagellates themselves, the closest group to metazoans, exhibit a facultative form of clonal multicellularity that sometimes depends on bacterial signalling (Fairclough et al. 2010; Alegado et al. 2012). Does this suggest that the ancestor of choanoflagellates and metazoans discovered a clonal form of multicellularity, with no ties to these other two forms of multicellularity (aggregation and coenocyte cellularization), and it was such a good discovery (or at least expensive to opt out of) that it became obligate? But many choanoflagellate lineages do not engage in multicellularity of any kind, and their ancestral ventures into this lifestyle may not be the basis for metazoan multicellularity (Suga and Ruiz-Trillo 2013). It might only be justified to say that all these lineages – ichthyosporeans, filastereans, choanoflagellates, metazoans, plus others that appear to be closely related and using yet other strategies (see Tikhonenkov et al. 2020) – were intensively exploring multicellularity and its potential, and all of them preserve their very different achievements to this day.

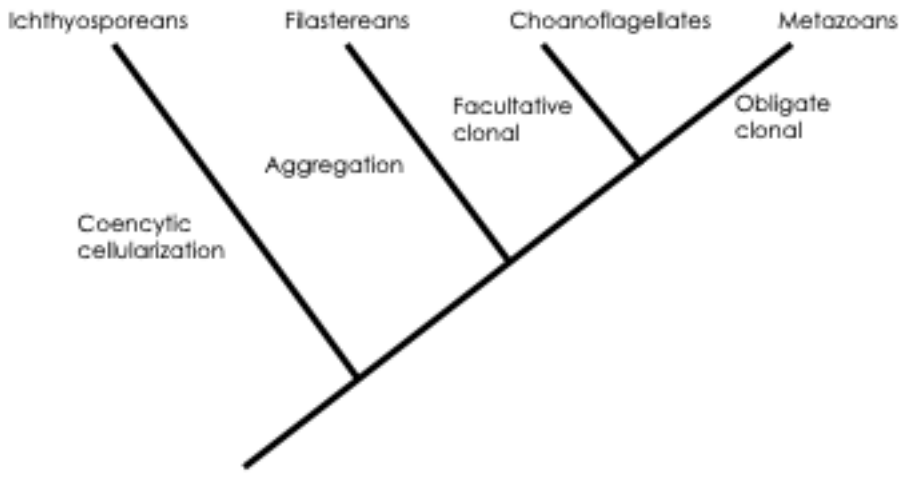


Figure 2.1: Holozoan experiments in multicellularity

2.3.2 Unifying versus particular explanations

Increasing comparative work shows that looking for common explanations of similar multicellular strategies is not necessarily a helpful strategy. For instance, although *Dictyostelium* multicellularity shares some similar genetic and architectural features with animal multicellularity, the phylogenetic distance between these forms points to convergence, rather than a shared ancestral state of multicellularity (Parfrey and Lahr 2013). Nevertheless, dictyostelid and myxobacterial capacities for multicellularity mean they are often used as models for morphogenesis (Kaiser 2003).

Experimental investigations of the origins of multicellularity necessarily focus on particular tractable organisms (e.g., Hammerschmidt et al. 2014; Ratcliff et al. 2012; 2013). Such studies are designed to be extrapolated: what is found in yeast, for instance, is suggested to have broader implications for how 'readily' and 'rapidly' multicellularity can evolve (Ratcliff et al. 2012, p. 109; Koschwanez et al. 2013). But just as intriguing is the fact that these newly emerged multicellular yeasts reproduce as multicellular units, without a unicellular stage (Ratcliff and Travisano 2014). In other experiments, the co-option of unicellular stages for minimizing genetic variation challenges the standard view that unicellular bottlenecks are adaptively central to the origin of clonal multicellularity (Ratcliff et al. 2013).

Although these experiments cannot recapitulate history, they seek generality by abstracting away from the experimental details of lab-evolved multicellularity. These abstractions might involve the relative importance of ecological versus genetic constraints (Ratcliff et al. 2013), mechanisms for cooperation (Bastians et al. 2016), and resource efficiencies (Koschwanez et al. 2013). But it is clear that such experiments produce novel occurrences of multicellularity that arise as the result of particular selection pressures, historical backgrounds, genetic capacities, and phenotypic proclivities. Such novelties might further undermine hopes of a unifying explanation for any multicellular phenomenon

### 2.3.3 Adaptive versus non-adaptive explanations

Although it is well-known that multicellularity has many independent origins and historical trajectories, there is still a tendency to seek general explanations of how multicellularity has emerged and persisted. A common feature of such accounts is an explanatory focus on adaptiveness. A standard list of common advantages for any form of multicellular organization includes predator resistance, new food sources (i.e., other organisms), reproductive efficiency, resource storage, recruitment of symbionts, sequestration of incompatible features (e.g., metabolic pathways, motility and reproduction), and phenotypic flexibility (see Grosberg and Strathmann 2007; Cavalier-Smith 2017; Umen 2014; Nagy, Tóth et al. 2018). And if at least some multicellularity with differentiated cells does not require a high genetic budget to originate and maintain (Nagy, Kovács, Krizsán, 2018), then the existence of many independent origins might be explained quite simply (i.e., low-cost exploration of phenotypic space, with potentially high payoff).

Although many experimental and natural-historical studies of multicellularity focus on explanations that emphasize advantages, at least as much if not more can be learned about multicellularity by considering the implications of disadvantages for both the origin and persistence of any particular form (Cavalier-Smith 2017). Non-adaptive accounts of multicellularity highlight biophysical processes that lead to lineages 'drifting' into multicellular explorations and leading in some cases to the co-option of features such as adhesion (Niklas and Newman 2020). Committed multicellularity, in which differentiation is spatial rather than temporal, means that the flexibility to switch between unicellular and multicellular states is lost, which may be risky in changing environments.

Relatedly, if indeed some lineages had a pre-existing toolkit for other functions that was co-opted for novel multicellular functions (Parfrey and Lahr 2013; Niklas and Newman 2020; Ratcliff et al. 2013), it might mean that some multicellularity takes an evolutionary road that is hard to back out of. Once certain tools get locked into the clonal construction of new forms of interdependent cellular organization, it might be difficult to put those tools back to work in old independent functions. Small population sizes of facultatively multicellular organisms might incur less stringent selection and thus persist despite modestly detrimental outcomes (Lynch 2007). Subsequently, if certain environments favour multicellularity even briefly, there could be disadvantages to maintaining unicellular options throughout the lifecycle of generations, and so these stages are lost and prove difficult to re-evolve (Libby et al. 2016). Despite some lineages managing to give up on clonal multicellularity, they are vastly outnumbered by the plants, animals, fungi and algae that were obliged to continue with a lifecycle of reduced complexity but morphology of greater complexity.

### 2.3.4 Explanatory implications of losing multicellularity

Although metazoans are sometimes referred to as possessors of 'unconditional multicellularity' (Schilde and Schaap 2013, p. 7), meaning all metazoans are multicellular, this universality has a few interesting aberrations. Microscopic myxozoans are the classic examples of animals giving up on complex body plans (but not complex lifecycles), where not only organs have been discarded along the evolutionary way, but also aerobic mitochondria (Chang et al. 2015; Yahalomi et al. 2020). Transmissible cancers are an extreme example of reversed multicellularity in a range of metazoans (e.g., dogs, Tasmanian devils, shellfish), in which clonal unicellular lineages have made their escape from obligatory multicellular origins (Murgia et al. 2006; Rebbeck et al. 2009). Some commentators go so far as to suggest human cancer cultures, selected and nurtured by biomedical researchers for generations, are also reduced metazoans, now living as 'protists' (Strathmann 1991).

Elsewhere, yeasts have convergently given up on multicellularity (e.g., *Saccharomyces*, *Schizosaccharomyces*), although they can recover it in certain conditions, meaning that perhaps they have managed to reverse a previously obligate state of multicellularity to a merely facultative one (Dickinson 2005; Nagy et al. 2017). Some unicellular green algae show evidence of derivation from multicellular lineages (Delwich and Cooper 2014). Cyanobacterial lineages have frequently lost and occasionally rediscovered multicellularity (Schirrmeister et al. 2011). These instances of reversion of multicellularity, although wide-ranging, are nevertheless fewer than all the independent origins, which makes multicellularity look like a trait that is harder to lose than to gain.

But rather than thinking only about the loss of multicellularity as a phenomenon that needs explaining, we might also want to think about the retention of unicellular stages in some facultatively multicellular lineages. What holds them back from a full-blown commitment to multicellularity? Why not give in to obligate clonal multicellularity? Even though lifecycle complexity in organisms with facultative multicellularity seems like hard work to maintain, it has persisted in some lineages for longer than the switch to simple lifecycles with a unicellular zygotic or spore stage. But seeing extensive cell differentiation in clonally multicellular organisms as some sort of advance is potentially problematic especially if the long-term future of life on Earth is considered. In all mass extinction events, large multicellular forms are the most prone to being wiped out (Mata and Bottjer 2012). Nevertheless, many discussions of the evolution of multicellularity proceed as if obligate clonal multicellularity is a state worth attaining, despite its vulnerability to major environmental changes.

## 2.4 Why do we value multicellularity?

It is a curious phenomenon that despite most life on Earth being unicellular, a great deal of value is placed on the emergence of multicellular life forms, and of those, very particular versions of multicellularity. For instance,

> 'One of the most remarkable events in evolutionary history was the emergence and radiation of eukaryotic multicellular organisms' (Niklas and Newman 2013, p. 41).
>
> 'Although multicellularity arose more than 20 times, the "spectacular" forms arose only in plants, animals and fungi' (Szathmáry 2015, p. 10108).

There are numerous justifications for why certain forms of multicellularity are so important and interesting.

> 'the evolution of complex multicellularity … is clearly where key questions of diversity and ecological success lie [rather than the origin of simple multicellularity]' (Knoll 2011, p. 221).
>
> 'Of all the transitions between levels of organization, the advent of multicellularity is perhaps the most interesting … Multicellularity completely redefines the concept of what is an individual organism, and has occurred independently dozens of times across all domains of life. Multicellularity represents a transition from the microscopic to the macroscopic world [and thus different responses to] physical laws. Multicellularity also enabled vast phenotypic expansion and diversification, primarily via cell differentiation and temporal development of morphological structures within an organism. And finally, multicellularity is most likely a necessary step along the evolutionary path to intelligence and consciousness' (Lyons and Kolter 2015, p. 21).

Quotes such as these suggest several reasons for valuing multicellularity and transitions to it: increasing diversity, adaptive complexity, and macroscopic size.

### 2.4.1 Diversity

The most basic reason for valuing multicellularity is that there are many instances of it (or even of just 'complex' multicellularity) and that it leads to further diversification in the form of more speciose lineages and greater exploration of phenotypic space. However, the same could be said of unicellularity, especially in terms of thermodynamic 'space' (Poole et al. 2003; Nealson and Conrad 1999), and we might think unicellular diversity has a higher chance of persisting when drastic changes occur to the Earth (Mata and Bottjer 2012). But in response it might then be argued that multicellularity is more adaptive in important respects.

### 2.4.2 Adaptive complexity

> 'Multicellularity is a major evolutionary innovation … [that] is a requisite for the development of adaptive complexity' (Herrero et al. 2016, p. 832).

But here we might ask whether there is less adaptive complexity in, say, unicellular organisms that have a range of metabolic capacities, all of which are rarely achieved by standard multicellular organisms. For example, many unicellular organisms can switch from autotrophy to heterotrophy, or from aerobic to anaerobic respiration (Kelly and Wood 2006). They can oxidize methane aerobically for breakfast and hydrogen anaerobically for dinner (Carere et al. 2017). Other populations of microorganisms might be defined by their proclivity to drink hydrogen, but have hidden tendencies to snack on glucose and sip alcohols (Schichmann and Müller 2016). More generally, numerous microbes can make extensive use of inorganic energy substrates, which is beyond the scope of large eukaryotes (Nealson and Conrad 1999). This metabolic diversity and flexibility is why microbes are dominant players

in most biogeochemical cycles. Versatility in one sphere (i.e., metabolism) but not others (i.e., size and shape) might be discounted if one sphere is intuitively valued more highly.

2.4.3 Macroscopic size

> 'Although most of the individual organisms living on Earth today are still unicellular, if all multicellular eukaryotes suddenly vanished from Earth, our planet would appear as barren as Mars' (Kirk 2005, p. 299)
>
> '[If we were to] remove the multicellular land plants … [and] get rid of … animals [and] multicellular fungi … [there would be an] empty landscape of bare soil dotted by microscopic photosynthetic bacteria and algae' (Ratcliff and Travisano 2014, p. 383).

The 'emptiness' postulated by such views seems to depend heavily on projections of familiar landscapes. It is highly likely that prior to the visual dominance of plants and animals, the Earth was a teeming mass of phototrophic microorganisms of every shade of green and red, forming mats in the shallows and turbid blooms in open waters (Butterfield 2015). The supposedly 'bare soil' was crusted, filmed and threaded by a variety of unicellular lifeforms, in all sorts of shades and shapes, with considerable biogeochemical impact (Wellman and Strother 2015; Lebandeira 2005; Horodyski and Knauth 1994). Some were probably coenocytes, and their large clusters would have added to the visual diversity. Rocks were dramatically stained by other microbial life, and ebbing and flowing glaciers dappled by conglomerations of photosynthesizers and other cold-tolerant microbes (Beraldi-Campesi 2013; Vincent et al. 2000). Admittedly, these many types of colourful and intricate communities were not visually similar to today's forests or grasslands, but the landscape would not have been devoid of displays of life or even beauty. And these lifestyles are as biome-defining and niche-creating as the existence of large plants, herbivores, and predators. In other words, it is not clear that claims about 'barrenness' can be justified beyond the fact that only certain visible lifeforms meet standard human expectations.

2.5 Conclusion

In short, using the term 'multicellularity' as if it refers to a particular phenomenon looks problematic. We know about many different origins and instances of multicellularity. We may be attuned to features they have in common rather than their differences and even uniqueness. This proclivity in turn might make overly broad any explanation of particular achievements of multicellularity, whether these achievements are historical or experimental. We are inclined to over-value certain forms of multicellularity, partly because of visibility and obvious impact on us as humans. However, there is no denying that the world we inhabit and perceive is one of large forms with extensive environmental impact, and that advancing theory and interpreting evidence for how such forms evolved is an utterly central project in evolutionary studies. The more that is learned about all the different instances of multicellularity and their origins, the more complete our understanding of evolution will be.

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