neuromechanics/control forward are to be had. It seems likely that principles emerging from *Caenorhabditis elegans*, zebrafish, and *Drosophila* may provide the next giant leaps in understanding.

Do you believe that there is a need for more crosstalk between biological disciplines? Yes! It's just good to be open-minded and chat to everybody — they often have different modes of thinking or just plain cool ideas when they see the stuff you've been looking at forever.

Do you think that there is too much emphasis on 'big data'-gathering collaborations as opposed to hypothesis-driven research by small groups? I think that what's implied here is that the big data-gathering collaboration is also a fishing expedition because otherwise these things need not be exclusive: you could be part of a big data-gathering collaboration that is hypothesis driven. I am thinking of neuroscience, where most seem to agree that a barrier is recording/manipulating lots of neurons simultaneously in disparate regions of the nervous system. You could have great, tidy hypotheses for how these ensembles should work and need big data to test them. But having come through neuroethology, I think that hypotheses are important, especially when a field is focused and has models of how things work — biology is just so complex that you have to whittle things down to move the edge of understanding forward (and I say that as someone who needs to do better at having *a priori* hypotheses). But then, a ton of great discoveries have come from natural curiosity, observing fascinating animal behavior and investigating its context or underlying mechanisms, sans hypotheses. Whether big data are needed for that kind of biology, I'm not sure. I love this question, and I wish that I had time to survey the history of science literature to see if there are clues to when we make the most rapid progress. But then, big data in its current form may have no older precedents.

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Essay

Could this pandemic usher in evolution's next major transition?

W. Ford Doolittle

Much discussion about the impact of the Covid-19 pandemic and whatever emerges as the 'new normal' has been psychological or political in nature, but there is a more inclusive evolutionary biological context in which we might understand it, ourselves, and our responsibilities to the planet.

The Major Transitions in Evolution, a book authored by the late John Maynard Smith and Eörs Szathmáry, was published a quarter-century ago [1]. Its publication was greeted with relief by many evolutionary biologists, because it legitimized putting some sort of positive spin on 'evolutionary progress'. Although many of us privately felt that life has become more sophisticated (or at the least, more complex) over the last few billions of years, we had been persuaded that such beliefs were inconsistent with a Darwinian perspective. Charles Darwin himself was not uncomfortable with the notion that creatures have gotten more finely adapted to their particular environments over time, but in the last half of the 20th century we had come to believe that what really drives evolutionary change overall is environmental change, a random force allowing for progression but not progress. Evolution tracks environmental change but has no inherent tendencies, we thought.

Steven Jay Gould, probably the most influential mid-century theorist for the public and practicing biologists alike and a champion of evolutionary 'contingency', was particularly down on the notion of progress. He wrote that it "is a noxious, culturally embedded, untested, nonoperational, intractable idea that must be replaced if we wish to understand the patterns of history" [2]. In his book *Wonderful Life* [3] he likened the evolution of life's complexity to a sort of random 'Drunkard's Walk'. Life started very simply of course and since complexity space is large, wound up some place more complex, but there was no driving force favoring the formation of complex organisms like ourselves from simple ones like bacteria. There was only contingency, he held, and most of us went along with him.

Evolutionary transitions as collectivizations

Maynard Smith and Szathmáry's book changed this thinking insofar as it described evolution as an almost inevitable series of major events — or sometimes similar major events occurring in parallel in different lineages. These major transitions are characterised by a subsuming of the evolutionary interests of lower-level units by higher-level collectives comprising several or many such units (Figure 1). This was thus indeed a kind of progressive ratchet, moving evolution towards ever higher levels of complexity and sophistication, by nesting individuals within collectives, as new, composite individuals. A sacrifice in independence or reproductive 'selfishness' of the units to the collective was a new evolutionary principle, Maynard Smith and Szathmáry argued. As they put it: "One feature is common to many of the transitions: entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it".

The Major Transitions in Evolution used as examples the incorporation of genes into chromosomes, of cyanobacteria and free-living bacteria plus their ultimate hosts into eukaryotic cells, the incorporation of individual lineages into species through the invention of inter-lineage recombination (sex), and the origin of multicellular organisms from unicellular organisms [1]. At transitional stages, there was a conflict of evolutionary interests to be overcome, and sometimes the higher-level entity still shows only what Maynard Smith and Szathmáry called 'contingent irreversibility'. For instance, some genes can free themselves from the yoke of control by chromosomes, becoming transposable 'jumping genes' or even viruses. Likewise, some

sexual species can revert to asexuality, and sometimes cellular lineages can start to replicate independently of the controls imposed by the multicellular organism of which they are part: we call that cancer.

Sometimes external biological or abiotic environmental stressors might be imagined to have established conditions favourable to a transition: competition between different individual gene families might have favoured their getting together as chromosomes, increased atmospheric oxygen might have driven the origin of nucleus-containing cells, competition with parasites might have favoured the evolution of sex, and the advantages of size and the evolutionary opportunities offered by cellular differentiation could have promoted the transition to multicellularity, which has occurred several times in several lineages.

There were also even higher-level transitions having to do with social organization. Maynard Smith and Szathmáry saw the origin of eusocial insects from solitary individuals or primate societies as examples. Cultural theorists have gone further, seeing a progression from bands (tribes), to chiefdoms (kingdoms) to nations and partially successful national alliances like the League of Nations or the UN, while the evolutionary ecologist Stephen Stearns suggested more than a decade ago that we are now "stalled part way through a major evolutionary transition from individual to group" [4]. Indeed, the irreversibility of cultural transitions is still highly 'contingent' in Maynard Smith and Szathmáry's sense.

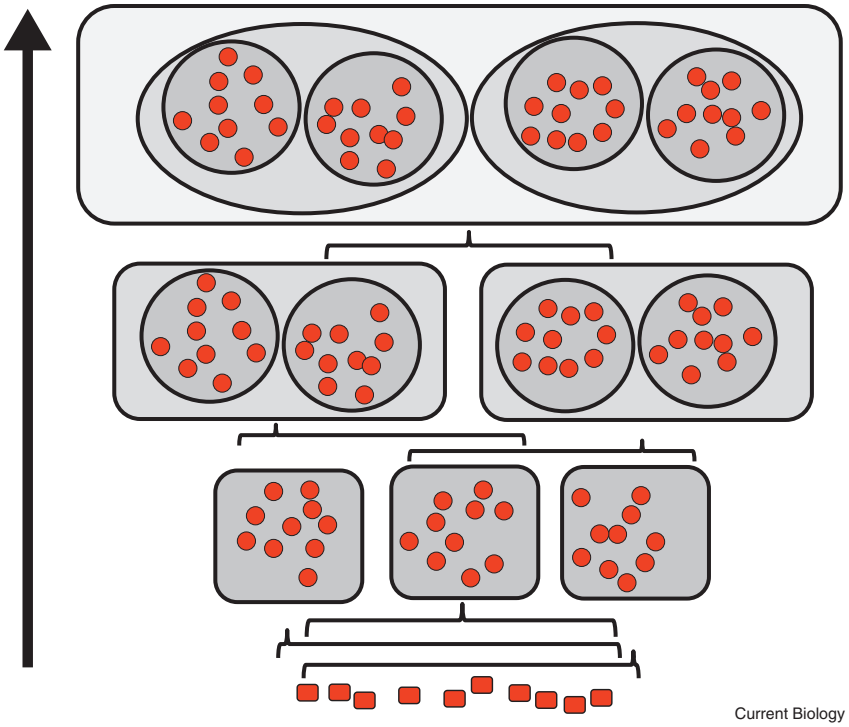

Figure 1. Major transitions in evolution.
At each transition, entities capable of independent reproduction (and thus with their own evolutionary trajectories) combine to produce collectives that reproduce and have new trajectories. In some cases, the transition is incomplete and lower level units can subvert collective interests (as in cancer). The social transition that Covid-19 might facilitate is as yet very incomplete. Arrow is time.

Covid-19 and collective integration

The current Covid-19 pandemic — ironically involving events at the lowest level of the biological hierarchy — is a stressor of unguessable strength and unknowable consequences: most of us cannot really get our minds around the potential impact or imagine where *Homo sapiens* is now heading. Political pundits have speculated about the new normal, and much of this speculation boils down to realizing that there are two main possibilities: either we revert to populist nationalisms and even racial tribalisms or we unite as an international collectivity, addressing not only Covid-19 but climate change and our species' deep socioeconomic divisions, these stressors now combining in unpredictable ways. The threat is global, but responses so far vary nation to nation, depending on leadership and local political forces

An essay by the ecological economist Simon Mair in *The Conversation* [5] further imagines a four-part grid (Figure 2), the two dimensions of which are response (centralized-to-distributed) and value (economics vs the protection of life). State capitalism and state socialism are the two centralized responses and barbarism and mutual aid are the distributed outcomes, and of course any real response will be a mix of the four, unpredictable as yet. Most first-world governments are at the moment drifting towards state socialism, but it's not clear how much economic damage can be sustained before state capitalism resurges as it seems now to be doing in the US and UK, and Hobbesian barbarism is always a horrible possibility — especially if these two versions of centralization are seen as inevitably in conflict.

Though we can look at all this politically and socioeconomically, there is as well the broader evolutionary biological perspective provided by Maynard Smith and Szathmáry. If what has happened in evolution (either biological or socio-cultural) is a sequence of subsummations of lower-level entities into collective, higher-level ones, entailing inter-level conflict and a sort of contingent irreversibility, then that may be happening once again, and again under stress, with an uncertain outcome. We are at the cusp. Indeed, the tensions we now see between populisms of the left and right could be interpreted as conflicts between allegiances to individual rights as opposed to collective responsibilities, not unexpected in such a subsummation.

And maybe this biological perspective is even, stepping back, a better and more informative, longer-term view. Certainly, it allows some perspectival distancing from the politics, though not ultimately excusing disengagement. Mair's two favored outcomes

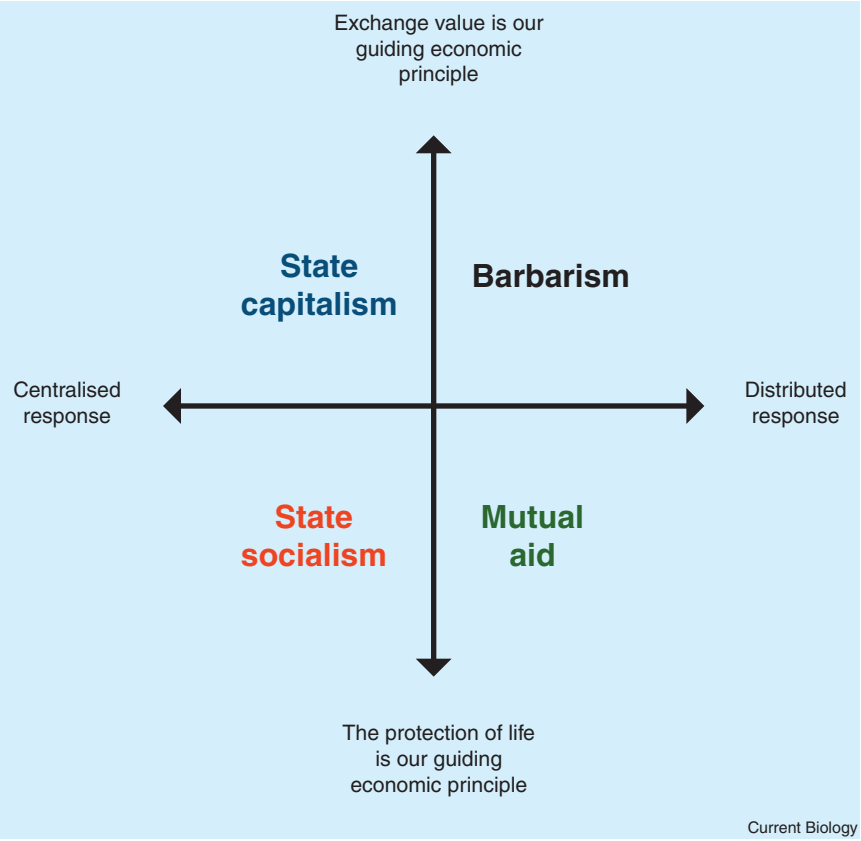

Figure 2. Four possible outcomes of the current crisis.
Reprinted with permission of the author, Simon Mair [5].

might correspond to the transitions represented by the origins of eukaryotes, in which evolutionarily separate but symbiotic (mutualist) entities fused into one individual with 'top-down' control (Mair's 'state socialism'), and the formation of ecosystems, sustained by the joint activities of many species ('mutual aid'). Either would entail our species functioning at a higher, collective level: a major transition in the making. This is not to say that such a collective response could not be nuanced to match local conditions, but the situation requires recognition that it is our species that is at risk, and that to save it may require a radical rethink of the relationships of individuals and collectives.

This is not just metaphorical thinking, biologizing to avoid political polarization. Perhaps the only way to survive this crisis, and maybe climate change and socioeconomic disparity, is to start acting as the single species that we are, rather than as the individual tribes or nations that we comprise.

In fact, we are a species embedded with and dependent on many others and so this transition is further unique in the following way. Because we are conscious agents, the collective of all species on Earth now becomes conscious, potentially capable of directing its own future. The 'we' in "we are all in this together" embraces more than just *Homo sapiens*. Tim Lenton and Bruno Latour stressed this in a recent article [6]:

> "According to Lovelock and Margulis's Gaia hypothesis, living things are part of a planetary-scale self-regulating system that has maintained habitable conditions for the past 3.5 billion years. Gaia has operated without foresight or planning on the part of organisms, but the evolution of humans and their technology are changing that. Earth has now entered a new epoch called the Anthropocene, and humans are beginning to become aware of the global consequences of their actions. As a result, deliberate self-regulation — from personal action to global geoengineering schemes — is either happening or imminently possible. Making such conscious choices to operate within Gaia constitutes a fundamental new state of Gaia, which we call Gaia 2.0.

Covid-19 is a consequence of human action. The larger our population and the more we invade the habitats of other species the more frequent will be such zoonotic diseases, and the more global are our travels the quicker these diseases will spread [7]. It's not that Gaia is deliberately punishing us. But it is that we still behave as if nations were our most inclusive units, and economics — not protection of life — was our purpose. We must 're-biologize' our thinking. We need to recognize that we are all part of one species and that this species is just one among many, singular only in being uniquely capable of understanding and changing the future of all life on the planet. If we can accomplish that, we will have witnessed the last (for now) and most inclusive (for now) of the major transitions in evolution. Whether such a biosphere-wide subsummation of evolutionary interests by a centralized bio-cultural entity, if it happens, will look more like Mair's 'state capitalism' or his 'state socialism' is anybody's guess. Perhaps an intermediate stage corresponding to a more robust and coordinated form of his 'mutual aid' is the best we can or should hope for now.

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