ASTROBIOLOGY
Volume 8, Number 1, 2008
© Mary Ann Liebert, Inc.
DOI: 10.1089/ast.2006.0115

Research Paper

Implications of an Anthropic Model of Evolution for Emergence of Complex Life and Intelligence

ANDREW J. WATSON

ABSTRACT

Structurally complex life and intelligence evolved late on Earth; models for the evolution of global temperature suggest that, due to the increasing solar luminosity, the future life span of the (eukaryote) biosphere will be "only" about another billion years, a short time compared to the ~4 Ga since life began. A simple stochastic model (Carter, 1983) suggests that this timing might be governed by the necessity to pass a small number, n, of very difficult evolutionary steps, with $n < 10$ and a best guess of $n = 4$, in order for intelligent observers like ourselves to evolve. Here I extend the model analysis to derive probability distributions for each step. Past steps should tend to be evenly spaced through Earth's history, and this is consistent with identification of the steps with some of the major transitions in the evolution of life on Earth. A complementary approach, identifying the critical steps with major reorganizations in Earth's biogeochemical cycles, suggests that the Archean-Proterozoic and Proterozoic-Phanerozoic transitions might be identified with critical steps. The success of the model lends support to a "Rare Earth" hypothesis (Ward and Brownlee, 2000): structurally complex life is separated from prokaryotes by several very unlikely steps and, hence, will be much less common than prokaryotes. Intelligence is one further unlikely step, so it is much less common still.

Key Words: Major transitions—Lifespan—Biosphere—Rare Earth—Critical steps—Earth history—Archean—Proterozoic. Astrobiology 8, xxx–xxx.

INTRODUCTION: LIFE SPAN OF EARTH'S BIOSPHERE

STANDARD SOLAR MODELS robustly predict that the luminosity of the sun is increasing. One such model, for example, purports a ~25% increase since the formation of the Solar System (Newman and Rood, 1977). Earth's surface temperature has been stabilized against increase by opposing effects, particularly negative feedbacks on temperature that operate via the reduction of the carbon dioxide atmospheric greenhouse (Walker *et al.*, 1981; Lovelock and Watson, 1982; Volk, 1987). Maintenance of Earth's present biosphere requires temperatures <50°C and at least ~10 ppm of atmospheric CO_2; so extrapolating to the future, the life span of the biosphere is likely to be limited by a combination of decreasing CO_2 and increasing temperature (Lovelock and Whitfield, 1982). In recent years, studies of in-

---

School of Environmental Science, University of East Anglia, Norwich, UK.

creasing sophistication (Caldeira and Kasting, 1992; Franck *et al.*, 2000; Lenton and von Bloh, 2001) have suggested that the future lifetime for the eukaryotic biota will be ~1 Ga, with a likely uncertainty of 0.5–1.5 Ga, which is substantially shorter than the period of ~4 Ga that has passed since life first appeared on the planet. Here I explore the idea that the realization that Earth's biosphere is now in its old age has implications for our understanding of the likelihood of complex life and intelligence arising on any given planet.

Figure 1 shows the future life span, according to a recent model (Bergman *et al.*, 2004), and illustrates the processes at work in the studies of the life span of the biosphere. This model is an attempt to synthesize information on the coupled behavior of the major elemental cycles (C, P, S, O, and N) that govern the concentration of CO_2 and oxygen in the atmosphere, and their influence on planetary temperature. It incorporates the concept of negative feedback, which was first discussed by Walker *et al.*, (1981) and extensively elaborated upon by Berner and colleagues (Berner *et al.*, 1983; Berner, 1991; Berner and Kothavala, 2001), whereby temperatures are stabilized by the atmospheric CO_2 concentration: removal of CO_2 from the atmosphere-ocean system is a result of the weathering of silicate minerals on the land surface, and these weathering processes are enhanced by increased temperature, biological activity, and runoff, all of which are positive functions of atmospheric CO_2 concentration. From the present onward, the increasing solar luminosity drives higher temperatures, which lead to more rapid weathering of silicates to carbonates, mediated by land vegetation. As a consequence, atmospheric CO_2 concentration drops to less than 100 ppm after about 300 million years. At about 800 million years, CO_2 concentration becomes so low that it begins to limit vegetation significantly (assumed to be C4 photosynthetic), which leads to a precipitous decline and demise of the biota at about 1.1 Ga.

The important assumptions that set the timescale for this outcome are the upper temperature limit for eukaryotic life, taken as ~50°C, and the requirement for CO_2 in the atmosphere. While there are many uncertainties in the details, the life-span prediction is relatively robust to changes in the model assumptions. It is difficult to extend the life-span prediction by adjusting the sensitivity of carbonate-silicate weathering to temperature because, for example, if this is made more sensitive, CO_2 declines and limits photosynthesis more severely; and if it is made less sensitive, the temperature increases more quickly, which limits the biota. These considerations suggest that the era of structurally complex macroscopic life on Earth will be limited to a further ~1 Ga, which will be succeeded by a period that will see the survival of thermophilic microbes but not present-day eukaryotes. In this respect, the last organisms to survive on Earth may be similar to some of the first to appear.

The question of the future life span of the biosphere has relevance to estimates of the likelihood that complex, perhaps intelligent, life evolves on a given planet. At present, Earth is the only example we have of a planet with life, and the fact that our own existence depends on Earth having developed complexity and intelligence introduces an anthropic "self-selection" bias into our sample of one (Bostrom, 2002). If we learned that

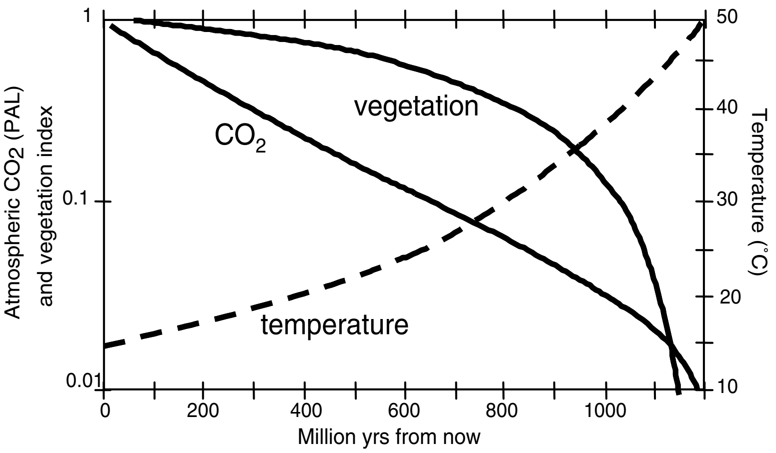

FIG. 1. Predictions of future atmospheric CO_2 concentration (in present atmospheric values or PAL) and global planetary temperature, and an index of land biota productivity from the COPSE model (Bergman *et al.*, 2004). The model has representations of the global biogeochemical cycles of carbon, oxygen, sulfur, nitrogen, and phosphorus. It is run forward in time with steadily increasing solar luminosity. Note the logarithmic axis for the CO_2 and vegetation indexes. The figure is redrawn from Bergman (2003).

the planet would be habitable for a set period and if we had evolved early in this period, then even with a sample of one, we might suspect that this suggested evolution from simple to complex and intelligent life was relatively likely to occur. By contrast, however, it is now believed that we evolved late in the habitable period; this suggests that our evolution is a comparatively unlikely occurrence.

DESCRIPTION AND EXTENSION OF CARTER'S MODEL

This dependence can be made more quantitative with the aid of a simple model that accounts for anthropic self-selection, which was introduced by Carter (1983). The model assumes that, on a planet such as Earth where observers eventually arise, the pace of this evolution is governed by the necessity to pass a number n (unknown *a priori*) of critical steps, which are defined as being intrinsically unlikely to occur in the time available. Each of these critical steps can only occur after the previous steps in the sequence have occurred. All other evolution is assumed to occur rapidly, such that the time taken for the necessary evolution between the steps does not affect their timing. The critical steps are assumed to occur stochastically, with uniform but unequal probabilities, $\lambda_1 \ldots \lambda_n$, and the property that they are intrinsically unlikely is expressed by the condition $\lambda_i t_h << 1$ for all λ_i, where t_h is the habitable lifetime of the planet. No other restriction is placed on the values of λ_i—in particular, they may differ by orders of magnitude, and individual λ_i may be arbitrarily small, so that the probability of the overall sequence might be very low indeed.

The model is, of course, a highly conceptualized and abstract account of evolution. There is no obvious basis, for example, for dividing evolutionary steps into "easy" and "hard" classes. More likely, there is a continuum of likelihoods that particular evolutionary pathways will occur, which range from the very likely [which therefore recur convergently in diverse settings (Conway Morris, 2003)] to the very rare, some of which may have far-reaching consequences. The critical step model is useful if, on the longest timescale appropriate to evolution on Earth, the pace of evolution is determined by a relatively few steps of the second kind. Conversely, it would not be useful if the timescale for evolution is set entirely by a long sequence of events, each of which is likely but takes some time, so that cumulatively the process is very slow. If this is the reason why evolution on Earth has taken so long, it would imply that many planets that are habitable for long enough would evolve intelligent animals. An explanation would then be needed for the "Fermi paradox"—why we see no evidence for abundant intelligent activity elsewhere in the cosmos.

The model assumes that there is at least one unlikely step in the evolution of intelligence, so it could be said to incorporate an inherently pessimistic view of the probability of this occurring. If the long, slow fuse idea is rejected, then this seems the only explanation for why it has taken so long for intelligence to evolve on Earth. Otherwise, it would have to be argued that evolution on Earth has been unusually slow, something for which there is no *a priori* evidence (Carter, 1983).

It needs to be clearly appreciated that there is no process deterministically governing when, or whether, the critical steps occur. Considering the set of all planets, the model assumes that on most of them none of the steps occur, and for those planets on which the first step occurs, the second occurs on only a few, and so on, so that only on a small subset do n steps occur. Furthermore, there is nothing special about "observerhood" in the context of the model. Any other property of organisms that is governed by a sequence of rare, random events could be modeled in the same way. For example, if the evolution of an organism that is able to breathe fluorine gas requires a sequence of rare evolutionary events, the same model could be used to investigate when in the history of their planets such organisms tend to appear, in the rare cases that they ever do.

The probability density function (PDF) of the n^{th} step in a sequence of length n steps (which I denote by $P_{n/n}$) is given by the following [See Appendix for a derivation. Barrow and Tipler (1986) also discussed the model, and this equation may be obtained by differentiating their cumulative probability equation 8.6]:

$$P_{n/n}(t) \approx K \prod_{i=1}^{n} \lambda_i t^{n-1} \tag{1}$$

Here, K is a normalization constant, and the approximation is valid if $t << 1/\lambda_i$, for all i. If only the small subset of planets in which intelligence does arise is considered, *e.g.*, those on which all n steps are completed in the interval 0–t_h, the normalization constant can be found by equating the integral of $P_{n/n}$ to 1, thus

$$P_{n/n}(t) = \frac{nt^{n-1}}{{t_h}^n} \tag{2}$$

where all the λ_i are cancelled through by the normalization. This PDF represents the probability as a function of time of an intelligent observer species evolving, given the certainty that it does so before t_h. For $n > 1$, it is weighted toward the end of the habitable period, and as Carter first derived, the expectation time for the species to evolve is

$$\langle t_{n/n} \rangle = \int_0^{t_h} tP_{n/n}(t)dt = \frac{n}{n+1}t_h$$

This expression quantifies the comment made above that a late evolution of intelligence suggests that this is an unlikely event. In fact, according to this simple model, it is not so much the low probability of a single event that leads to this conclusion but the requirement that several such events must independently occur in sequence. The larger the number of such events required to reach a given complexity, the later, on average, it will occur.

If the earliest time at which Earth was habitable were 4 Ga and the latest time at which it will be habitable is 1 Ga in the future, a "best guess" for n in the case of humans on Earth is 4. Carter, writing before the studies that constrain the future life span of the biosphere, assumed a future life span of ~5 Ga and obtained a best fit for n of 1. The revised, higher value fits much better with a number of independent approaches to the broad-scale structure of evolution, as discussed further below.

Uncertainty on this number arises first because the future life span might be shorter or longer. If the life span is only 0.5 Ga, for example, the best fit for n would be 8. Second, uncertainty arises because, in any particular realization, the timing of a given step will not correspond exactly to its expectation time, this being only the average that would be obtained given many realizations. Large values, however, can be ruled out with confidence. For example, for the case of our evolution on Earth, Equation 2 can be used to show that $n > 10$ is ruled out with >90% confidence if we are now at $0.8t_h$. The conclusions from the model are unaffected even should technologically able observers have the capability to extend the life span of the biosphere (by, for example, placing giant mirrors in space or colonizing Mars), providing the "natural," non-extended estimate of the habitable period t_h is used in the model calculations.

Starting from Equation 2, I now derive the PDFs for the earlier steps in the sequence and express the joint probability of a sequence in which the m^{th} event occurs at time t and, in addition, a further n–m events occur after t with the last one occurring at t', as the product of two PDFs like Equation 2. The PDF of interest is then that joint probability integrated over all possible values of t':

$$P_{m/n}(t) \propto P_{m/m}(t) \int_t^{t_h} P_{n-m/n-m}(t'-t)dt'$$

$P_{m/m}$ is proportional to t^{m-1} and $P_{n\text{-}m/n\text{-}m}$ is proportional to $(t'-t)^{n\text{-}m-1}$, so it can be written:

$$P_{m/n}(t) \propto t^{m-1} \int_t^{t_h} (t'-t)^{n-m-1}dt' = K_1 t^{m-1}(t_h - t)^{n-m} \tag{3}$$

where a new normalization constant, K_1, is introduced. To find this constant, integration by parts is used over the range 0–t_h, and the integral is equated to 1, finally obtaining:

$$P_{m/n}(t) = \frac{n!}{(n-m)!(m-1)!} \frac{t^{m-1}(t_h-t)^{n-m}}{{t_h}^n} \tag{4}$$

(Figure 2 shows the shapes of these PDFs for the cases where n = 1, 2, 3 and 4.) Equation 4 can be used to obtain the expectation time for occurrence of the m^{th} term in a series of length n, a generalization of Carter's result above:

$$\langle t_{m/n} \rangle = \int_0^{t_h} tP_{m/n}(tdt = \frac{m}{n+1}t_h$$

On average, therefore, the steps should tend to be spaced evenly through the history of life on the planet. This spacing is quite independent of the values of the individual λ_i, providing these satisfy the criterion that they are much smaller than $1/t_h$. Thus, even if one step was very many orders of magnitude harder than all the others, it would be impossible to tell which it was by considering their timing alone. This property of even spacing was first appreciated by R. Hanson*, who used Monte

---

*R. Hanson, "Must early life be easy: the rhythm of major evolutionary transitions." Available online at http://hanson.gmu.edu/hardstep.ps

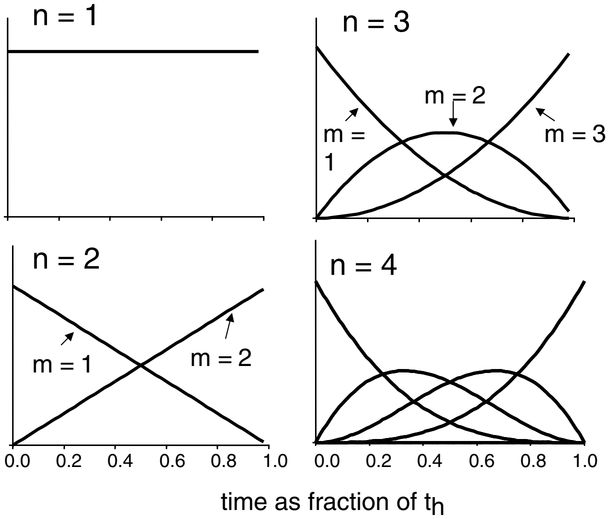

FIG. 2. Probability distributions from Equation 3 as a function of fractional time t/t_h, for n = 1, 2, 3, and 4.

Carlo simulations, and it has also been discussed by Bostrom (2002). Flambaum (2003) apparently independently arrived at a similar result (with, however, n replacing $n + 1$ in the denominator) by maximizing the probability that the sequence of n transitions occurs in the available time.

CRITICAL STEPS AS MAJOR TRANSITIONS IN EVOLUTION

Several routes for identifying candidates for the critical steps are possible, depending on what are considered to be the major constraints on the evolution of complexity. Here I offer an example from the perspective of evolutionary biology and, below, offer a second example from a more geological–Earth system perspective. The model is applicable regardless of the mix of constraints, provided that these lead to the evolution of complexity being paced by stochastic, low-probability events.

Table 1 shows the "major transitions of evolution" as described by Maynard Smith and Szathmáry (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995). These are transitions in which molecules or organisms combine to form more complex entities, which thereafter reproduce as a single unit. There is no reason *a priori* to expect these transitions to be critical in the sense of the model (*e.g.*, so unlikely that they would not be expected to occur for billions of years). Nevertheless, only 1 of the 8 (formation of colonies from individuals) seems definitely to have occurred more than once in the history of life and can be excluded on those grounds, which leaves a 7-step sequence.

Table 1 gives estimates for when the Szathmáry–Maynard Smith transitions occurred, based on inferences from the fossil record (almost none of them uncontroversial). Also tabulated are probabilities calculated from a model with a 7-step sequence constrained to last from 4 Ga before the present (assuming that continuing bombardment made the planet uninhabitable before that time) to 1 Ga in the future. The tabulated val-

TABLE 1. THE MAJOR TRANSITIONS IN EVOLUTION, AFTER MAYNARD SMITH AND SZATHMÁRY (MAYNARD SMITH AND SZATHMÁRY, 1995; SZATHMÁRY AND SMITH, 1995), WITH PROBABILITIES CALCULATED FROM THE PDFS GIVEN BY EQUATION 4, AS DESCRIBED IN THE TEXT

Transition	*Possible critical step?*	*Time of occurrence (before present)*	*Probability that step occurs at or before observed time*	
			7-step model	*5-step model*
1. Replicating molecules to populations of molecules	yes	<3.5 Ga	52%	—
2. Unlinked replicators to chromosomes	yes	<3.5 Ga	15%	—
3. RNA as gene and enzyme to DNA and protein (genetic code)	yes	<3.5 Ga	2.6%	41%
4. Prokaryotes to eukaryotes	yes	2.5–1.5 Ga	29%	66%
5. Asexual clones to sexual populations	yes	2.5–1.5 Ga	9.6%	32%
6. Protists to animals, plants, and fungi (cell differentiation)	yes	1–0.6 Ga	22%	41%
Solitary individuals to colonies (non-reproductive castes)	no	0.4–0 Ga?	—	—
7. Primate societies to human societies (language)	yes	0.001 Ga	21%	33%

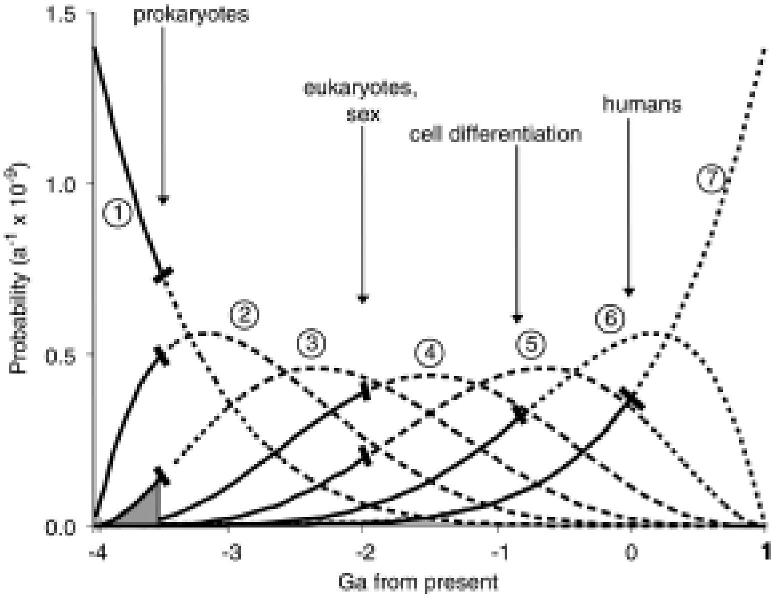

FIG. 3. Probability distributions in the 7-step model discussed in the text and in Table 1. The breaks and change from solid to dotted lines indicate where the corresponding Szathmáry–Maynard Smith transition is assumed to occur for the probabilities given in the table, and the illustrative timing of major events is also shown by the arrowed times. Note that for the third transition, the constraint that prokaryotes exist by 3.5 Ga means that the transition must occur in the tail of the distribution, with a probability <3% (shaded area).

ues are probabilities that the events would occur at, or before, the time they were actually observed (taken as the midpoint when a range is given). A very low, or very high, probability here indicates that the event is in one or the other tail of the PDF, hence a poor fit to the model. Figure 3 shows graphically the PDFs for this 7-step sequence, compared to the timing of the events. The major transitions that occur after prokaryotic life was established are well spaced throughout Earth history and are in a pattern consistent with their identification as critical steps. The relatively low probability of steps 6 and 7 occurring as early as observed reflects the fact that 7 is rather higher than the "best guess" value of 4 for *n*. However, under commonly accepted assumptions about early life, the early part of this sequence does not fit the model well. Given the evidence for the existence of prokaryotes by 3.5 Ga (Schopf, 2006), the first 3 steps are constrained to occur before 10% of the available time has passed. The probability of this occurring is <3% and is represented by the small shaded area of the tail of the distribution for the third step in Fig. 3.

The assumption that the planet was not continuously habitable before 4 Ga may be too restrictive. For example, there is evidence that there was liquid water on the planet by about 4.3 Ga (Mojzsis *et al.*, 2001), and some have argued that aspects of the accretion may actually have been beneficial to the early stages of evolution (Cockell, 2006). If the later bombardment was insufficient to sterilize the planet, then the earliest time of habitability might be moved back to 4.4 Ga, which allows, at maximum, 0.9 Ga for these steps to have occurred. Even in this case, however, the probability of passing three critical steps before 3.5 Ga remains <10%. By contrast, if a less conservative approach is taken and the isotopic signature of carbon granules in the Isua formation (>3.7 Ga) is interpreted as evidence for prokaryotic life (Rosing, 1999), and the end of the late bombardment at ~3.85 Ga is taken as the earliest point after which Earth was continuously habitable, then the probability of occurrence of three steps in this time interval falls to $<10^{-3}$.

These low probabilities reflect the well-known problem of the apparently rapid establishment of life on Earth. There are several possible resolutions of this problem. For example, life could have evolved elsewhere, on Mars for instance, over a less constrained time period (Davies, 2003). Or prokaryote life may evolve readily on a timescale of ~0.1 Ga so that none of these steps are critical in the sense of Carter's model. However, the model fits best if there is one, and only one, critical step involved in evolution to the prokaryote stage, followed later by several well-spaced difficult steps in the subsequent lineage that ends with humans. The model then provides an anthropic explanation for why the first evidence for prokaryotes is observed at a relatively early stage on Earth—the existence of several further, unrelated, and difficult steps later in the sequence means that an early occurrence of the first step is most likely to be observed, no matter how hard that is. The probabilities associated with the resulting 5-step sequence are recalculated in the last column of Table 1; this is assuming that only one of the first 3 of the Szathmáry–Maynard Smith transitions is critical. In this case, the observed dates for all the steps are comfortably near the centers of their respective distributions.

DOES THE EARLY ORIGIN OF LIFE ON EARTH CONSTRAIN THE ABSOLUTE PROBABILITY OF LIFE ORIGINATING ON OTHER PLANETS?

Lineweaver and Davis (2002) developed a quantitative argument to treat this question. They adopted a model of a repeated lottery, where biogenesis corresponds to winning at least once. If the chance of winning is unknown *a priori*, it can be constrained by an observation of how many times a gambler has to enter the draw before the first time he or she wins. The early date for biogenesis on Earth leads to the prediction of a high probability for biogenesis in this model. Lineweaver and Davis calculated, for example, that the probability of biogenesis is >13% at the 95% confidence interval.

The results discussed here support the view (Flambaum, 2003) that this is an overestimate because it does not take into account the several further difficult steps that are necessary to get from biogenesis to "observerhood." In terms of the lottery analogy, we need to condition our observations on winning not just the lottery of biogenesis, but several subsequent lotteries as well, in which tickets are only issued to those who have won in the previous round. In such a model, the constraint on absolute probability given by an early win in the first round becomes rapidly less useful as further rounds are added.

To be more quantitative, I have included below a means by which to test against the assumption that there is only one critical step in the evolution to the stage implied by the earliest evidence for life on Earth. The constraint on the absolute probability of biogenesis becomes useful only if biogenesis occurred much more rapidly on Earth than the expectation time to the first step in the stochastic model: $t_1 << t_h/(n + 1)$. Taking the best-guess values of $n = 4$ and $t_h = 5$ Ga, this translates to $t_1 << 1$ Ga. For small values of t, the probability that the first step should occur before t is approximately equal to nt/t_h. Thus $P_{(1/4)} < 0.1$ for $t_1 < 0.125$ Ga, and the random model at the 90% confidence level can be rejected if the time for biogenesis was shorter than this. Lineweaver and Davis estimated the time to biogenesis as $0.1^{+0.5}_{-0.1}$ Ga. If the most likely figure or lower end of this range is taken into consideration, their broad idea remains valid even after accounting for the later difficult steps: one would conclude, using our model with $n = 4$ and $t_h = 5$ Ga, that biogenesis occurred unusually quickly and, therefore, is probably relatively common in the universe, though the actual probabilities calculated by Lineweaver and Davis would require adjustment. On the other hand, toward the upper end of the range the constraint is of little use. The probability of biogenesis could be arbitrarily small, but it would still be expected to occur this early.

In their reply to Flambaum, Lineweaver and Davis (2003) discussed the critical step model. As they pointed out, if biogenesis is sufficiently unlikely to qualify as a (single) critical step, then the model predicts that the period between Earth's first becoming continuously habitable and biogenesis should be of the same order as the habitable period that remains after observers evolve. In my view, I cannot at present rule out that the time to biogenesis is ~0.5 Ga; therefore, no firm conclusion can be drawn as to whether biogenesis might be a common event on other planets. However, the discussion illustrates that a modest improvement in our knowledge of the timetable for biogenesis on Earth does have the potential to constrain the probability of biogenesis elsewhere, if it happens to be in the right direction, for example, pointing to life arising on a sufficiently short timescale to be inconsistent with the critical step model.

In his unpublished paper on the study of the critical-step model (cited above) by way of Monte Carlo simulations, Hanson was the first to point out that the model could yield a natural explanation for why biogenesis might have occurred early on Earth even if it is an unlikely event. He also discussed the possible correspondence between critical steps and the Szathmáry–Maynard Smith evolutionary transitions, noting that the clustering of 3 transitions before the earliest fossil evidence for life argued against that interpretation.

CRITICAL STEPS AS REORGANIZATIONS OF THE EARTH SYSTEM

Catling *et al*. (2005) argued that, for energetic reasons, the establishment of a high atmospheric oxygen concentration is a *sine qua non* for complex life and intelligence to evolve on any planet. On Earth, there is evidence that oxygen rose to its present value in 2 steps (Holland, 2006): the first at the Archean-Proterozoic transition beginning at ~2.4 Ga when it rose to $\sim10^{-3}$ atm, and the second at the Proterozoic-Phanerozoic boundary when it rose to essentially modern values, $\sim10^{-1}$ atm. These transitions involved major reorganizations in the carbon and nutrient cycles of the planet, with the buildup of a gas in the atmosphere that was potentially highly toxic. Both transitions seem to have been associated with repeated severe glaciations and may have been accompanied by extinctions, followed by radiation of new forms once the global climate stabilized. The number of these known transitions, which are sufficiently evenly spaced in time between the origin of life and the present, fits the criteria for critical events in Carter's model; and it is tempting to identify them, as such, as an alternative to the strictly evolutionary biological approach explored above.

The ultimate cause of the first of these transitions was the evolution of oxygenic photosynthesis. Though Kopp *et al*. (2005) recently argued that this event immediately predates the atmospheric oxidation, it is more generally thought to have originated before 2.7 Ga, on the strength of biomarker evidence for cyanobacteria of that time (Brocks *et al*., 2003). Models of Archean biogeochemical cycling suggest that oxygenic photosynthesis might have led to oxidation of the atmosphere only after a lengthy period during which the surface environment became oxidized due to hydrogen escape (Catling *et al*., 2001), which eventually led to a sudden switch from very low to comparatively high atmospheric oxygen (Goldblatt *et al*., 2006). Oxygenic photosynthesis appears to have evolved only once. The photosystem II water-oxidizing complex, which is the core of the enzymatic reaction responsible, appears to have remained unchanged over billions of years (Dismukes *et al*., 2001). This is despite the fact that it is tremendously useful metabolically (utilizing as it does sunlight and the 2 most abundant volatiles on the planet, both to fix carbon and provide energy). The conservative nature of the basic chemistry has been ascribed to the complexity of the system required to catalyze this thermodynamically very unfavorable process, which involves a 4-electron, 4-proton coupled reaction with the absorption of 8 photons per molecule of oxygen released (Dismukes *et al*., 2001). As such, the sequence of changes that began with the origin of oxygenic photosynthesis is a candidate for an intrinsically unlikely, critical step.

The cause of the second transition near the end of the Proterozoic has been suggested to be an increased efficiency in the chemical weathering of continental rocks. This also can be traced to biological innovations, in this case the evolution of eukaryotes [another step arguably in the "difficult" category, see Margulis *et al*. (2006) and Embley and Martin (2006) for recent discussions], which led, after a considerable time, to cell differentiation and the origin of fungi and plants. Early lichens were able to survive on bare rocks by weathering nutrients from them, which led to enhanced nutrient availability (Lenton and Watson, 2004) and carbon burial (Kennedy *et al*., 2006), both of which tend to force an increase in atmospheric oxygen.

Though the biological advances that initiated both of these transition periods may have been related to evolutionary inventions that occurred at specific points in time, the transitions took hundreds of millions of years to complete before a new dynamically steady state of the biogeochemical system emerged. Presumably, this achievement of stability with a new and more energetic biosphere was by no means inevitable and may not even have been very likely. There is evidence that, at both transitions, repeated climatic catastrophes in the form of global glaciations were triggered. It seems possible, therefore, that these transitions would have come to nothing with the extinction of the organisms responsible for the new invention and perhaps the eradication of many (or all) other organisms on the planet as well.

CONCLUSION

The critical-step model has not been widely discussed by evolutionary or paleobiologists.

One reason for this may be the conclusion originally reached by Carter (1983), that there was only 1 such step or, at most, 2, based on the assumption that we are presently only midway through the life span of the biosphere. This result is quite difficult to square with what is known about evolution on Earth. It implies, for instance, that the origin of what we call intelligence—the transition which separates humans from the other apes—is just about the most unlikely event to have happened in the history of life. However, the history of life includes increases in structural and genetic complexity concentrated in certain major transitions (Szathmáry and Maynard Smith, 1995) that can be correlated with major changes in the fossil record (Schopf, 1992) and upheavals in the biogeochemistry of the whole Earth system (Lenton *et al.*, 2004). These earlier transitions appear, on the face of it, to have been of equal or greater difficulty than the origin of human intelligence.

The recognition that Earth's biosphere is in its old age, such that the critical-step model allows a larger number of these events, resolves this problem and suggests that a re-examination of evolution on Earth in light of the model may be worthwhile. According to the analysis described here, the difficult steps that have paced evolution at the longest timescale have occurred at ~1 Ga intervals. This suggests that the penultimate step before the origin of observers (ourselves) on Earth was around the time of the late Proterozoic and may have been the differentiation of the eukaryotic kingdoms of plants, animals, and fungi. To reach that point, several previous difficult steps were passed; so complex life may be a rare phenomenon and observers rarer still. On the other hand, the rapid establishment of life on Earth after its formation may indicate that simple microbial life is relatively common. These conclusions lend some theoretical support to the Rare Earth hypothesis of Ward and Brownlee (2000).

It is worth emphasizing that, while I have focused on the set of steps that leads to intelligence, this is in a sense an arbitrary choice dictated by our special interest in this defining property of humans. The critical step model is quite general and could be applied to any other set of steps. For example, suppose we were interested in the evolution of elephant-like animals and considered the possession of a trunk as the most important attribute an organism could have. Suppose further, that the evolution of a trunk requires one unlikely step beyond those required for the evolution of complex animals. The model could then be used to predict the probability distribution for the time of appearance of animals with trunks within the set of all planets on which animals evolve. As it happens, this would be identical to the distribution for intelligent observers within *their* set of planets, as has been discussed, since they appear to require the same number of critical steps.

While the existence of transitions to increasingly complex life-forms through evolutionary time is widely recognized, there seems no obvious process within evolution itself to explain this directionality. The view that evolution involves a predictable progression, such that the emergence of intelligence is inevitable, is today generally considered to be overly anthropocentric [though Conway Morris (2003) put forward a well-argued case for it]. There are numerous examples where complex traits have apparently been lost from organisms, and the question of whether increases in complexity are in fact any more intrinsically likely than decreases remains unresolved (McShea, 2001). From the perspective adopted here, this appearance of evolution as a monotonic "progress" toward ourselves results from "anthropic self-selection bias" (Bostrom, 2002). In this case, there is no need to postulate any directionality to evolution; and, in general, the kind of outcome seen on Earth may be vanishingly unlikely. However, observers are necessarily complex, and only on those rare planets on which complex creatures happen to evolve can there exist observers who ask questions about evolution and care about the answers.

ACKNOWLEDGMENTS

I thank Tim Lenton, Noam Bergman, Colin Goldblatt, Jackie Watson and Simon Conway Morris for helpful discussion and critique of these ideas.

ABBREVIATION

PDF, probability density function.

APPENDIX: DERIVATION OF EQUATION 1

The critical steps are assumed to occur stochastically, with uniform (but not necessarily equal) probabilities, $\lambda_1 \ldots \lambda_n$, and the property that they are intrinsically unlikely is expressed by the condition $\lambda_i t_h << 1$ for all λ_i, where t_h is the habitable lifetime of the planet. The probability of the first step occurring per unit time is

$$P_1(t) \propto \lambda_1$$

The joint PDF of 2 events occurring, the first at time t' and the second at a later time t is:

$$P_{12}(t,t') \propto \lambda_1\lambda_2$$

and the PDF of the second event is obtained by integrating this expression over all possible values of t', *i.e.*, from 0 to t:

$$P_{2/2}(t) \propto \lambda_1\lambda_2 \int_0^t dt' = \lambda_1\lambda_2 t$$

where the notation $P_{2/2}$ for this PDF signifies that it refers to the second event in a sequence of 2 events. Strictly, only the first occurrence of either event is of interest, but provided consideration is restricted to time periods $<< 1/\lambda$, the probability of more than one occurrence of a step can be neglected, and this expression is valid.

The PDF for the third event in a sequence of 3 can similarly be found:

$$P_{3/3}(t) = \int_0^t P_{2/2}(t')P_3(t')dt' \propto \lambda_1\lambda_2\lambda_3 \int_0^t t dt' = \lambda_1\lambda_2\lambda_3 t^2/2$$

and the formula deduced for the PDF of the n^{th} step in a sequence of n steps:

$$P_{n/n}(t) \approx K \prod_{i=1}^{n} \lambda_1 t^{n-1}$$

which is Equation 1 in the text. $\propto$ has been replaced by equality, and K, a normalization constant, has been introduced.

REFERENCES

Barrow, J.D. and Tipler, F.J. (1986) *The Anthropic Cosmological Principle*, Oxford University Press, Oxford.

Bergman, N.M. (2003) COPSE: a new biogeochemical model for the Phanerozoic. PhD thesis, University of East Anglia, Norwich.

Bergman, N.M., Lenton, T.M., and Watson, A.J. (2004) COPSE: a new model of biogeochemical cycling over Phanerozoic time. *Am. J. Sci.* 304, 397–437.

Berner, R.A. (1991) A model for atmospheric CO_2 over Phanerozoic time. *Am. J. Sci.* 291, 339–376.

Berner, R.A. and Kothavala, Z. (2001) GEOCARB III: A revised model of atmospheric CO_2 over Phanerozoic time. *Am. J. Sci.* 301, 182–204.

Berner, R.A., Lasaga, A.C., and Garrels, R.M. (1983) The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *Am. J. Sci.* 283, 641–683.

Bostrom, N. (2002) *Anthropic Bias: Observer Self-Selection Effects in Science and Philosophy*, Routledge, New York.

Brocks, J.J., Buick, R., Summons, R.E., and Logan, G.A. (2003) A reconstruction of Archean biological diversity based on molecular fossils from the 2.78 to 2.45 billion-year-old Mount Bruce Supergroup, Hamersley Basin, Western Australia. *Geochim. Cosmochim. Acta* 67, 4321–4335.

Caldeira, K. and Karting, J.F. (1992) The life-span of the biosphere revisited. *Nature* 360, 721–723.

Carter, B. (1983) The anthropic principle and its implications for biological evolution. *Philos. Trans. R. Soc. Lond., A* 310, 347–363.

Catling, D.C., Zahnle, K.J., and McKay, C.P. (2001) Biogenic methane, hydrogen escape, and the irreversible oxidation of early Earth. *Science* 293, 839–843.

Catling, D.C., Glein, C.R., Zahnle, K.J., and McKay, C.P. (2005) Why O_2 is required by complex life on habitable planets and the concept of planetary "oxygenation time." *Astrobiology* 5, 415–438.

Cockell, C.S. (2006) The origin and emergence of life under impact bombardment. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 361, 1845–1856.

Conway Morris, S. (2003) *Life's Solution: Inevitable Humans in a Lonely Universe*, Cambridge University Press, Cambridge.

Davies, P.C.W. (2003) Does life's rapid appearance imply a martian origin? *Astrobiology* 3, 673–679.

Dismukes, G.C., Klimov, V.V., Baranov, S.V., Kozlov, Y.N., DasGupta, J., and Tyryshkin, A. (2001) The origin of atmospheric oxygen on Earth: the innovation of oxygenic photosynthesis. *Proc. Natl. Acad. Sci. U.S.A.* 98, 2170–2175.

Embley, T.M. and Martin, W. (2006) Eukaryotic evolution, changes and challenges. *Nature* 440, 623–630.

Flambaum, V.V. (2003) Comment on "Does the rapid appearance of life on Earth suggest that life is common in the universe?" *Astrobiology* 3, 237–239.

Franck, S., Block, A., von Bloh, W., Bounama, C., Schellnhuber, H.J., and Svirezhev, Y. (2000) Reduction of biosphere life span as a consequence of geodynamics. *Tellus, B, Chem. Phys. Meteorol.* 52, 94–107.

Goldblatt, C., Lenton, T.M., and Watson, A.J. (2006) Bistability of atmospheric oxygen and the Great Oxidation. *Nature* 443, 683–686.

Holland, H.D. (2006) The oxygenation of the atmosphere and oceans. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 361, 903–915.

Kennedy, M., Droser, M., Mayer, L.M., Pevear, D., and Mrofka, D. (2006) Late Precambrian oxygenation: inception of the clay mineral factory. *Science* 311, 1446–1449.

Kopp, R.E., Kirschvink, J.L., Hilburn, I.A., and Nash, C.Z. (2005) The Paleoproterozoic snowball Earth: a climate disaster triggered by the evolution of oxygenic photosynthesis. *Proc. Natl. Acad. Sci. U.S.A.* 102, 11131–11136.

Lenton, T.M. and von Bloh, W. (2001) Biotic feedback extends the life span of the biosphere. *Geophys. Res. Lett.* 28, 1715–1718.

Lenton, T.M. and Watson, A.J. (2004) Biotic enhancement of weathering, atmospheric oxygen and carbon dioxide in the Neoproterozoic. *Geophys. Res. Lett.* 31, L05202.

Lenton, T.M., Schellnhuber, H.J., and Szathmary, E. (2004) Climbing the co-evolution ladder *Nature* 431, 913.

Lineweaver, C.H. and Davis, T.M. (2002) Does the rapid appearance of life on Earth suggest that life is common in the universe? *Astrobiology* 2, 293–304.

Lineweaver, C.H. and Davis, T.M. (2003) On the nonobservability of recent biogenesis. *Astrobiology* 3, 241–243.

Lovelock, J.E. and Watson, A.J. (1982) The regulation of carbon dioxide and climate: Gaia or geochemistry. *Planet. Space Sci.* 30, 795–802.

Lovelock, J.E. and Whitfield, M. (1982) Life-span of the biosphere. *Nature* 296, 561–563.

Margulis, L., Chapman, M., Guerrero, R., and Hall, J. (2006) The last eukaryotic common ancestor (LECA); acquisition of cytoskeletal motility from aerotolerent spirochetes in the Proterzoic Eon. *Proc. Natl. Acad. Sci. U.S.A.* 103, 13080–13085.

Maynard Smith, J. and Szathmáry, E. (1995) *The Major Transitions in Evolution*, W.H. Freeman, Salt Lake City.

McShea, D.W. (2001) The minor transitions in hierarchical evolution and the question of a directional bias. *J. Evol. Biol.* 14, 502–518.

Mojzsis, S.J., Harrison, T.M., and Pidgeon, R.T. (2001) Oxygen isotope evidence from ancient zircons for liquid water at the Earth's surface 4,300 Myr ago. *Nature* 409, 178–181.

Newman, M.J. and Rood, R.T. (1977) Implications of solar evolution for Earth's early atmosphere. *Science* 198, 1035–1037.

Rosing, M.T. (1999) C-13-depleted carbon microparticles in >3700-Ma sea-floor sedimentary rocks from west Greenland. *Science* 283, 674–676.

Schopf, J.W. (1992) *Major Events in the History of Life*, Jones and Bartlett Publishers, Boston.

Schopf, J.W. (2006) Fossil evidence of Archaean life. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 361, 869–885.

Szathmáry, E. and Maynard Smith, J. (1995) The major evolutionary transitions. *Nature* 374, 227–232.

Volk, T. (1987) Feedbacks between weathering and atmospheric CO_2 over the last 100 million years. *Am. J. Sci.* 287, 763–779.

Walker, J.C.G., Hays, P.B., and Kasting, J.F. (1981) A negative feedback mechanism for the long-term stabilization of Earth's surface temperature. *J. Geophys. Res.* 86, 9776–9782.

Ward, P.D. and Brownlee, D. (2000) *Rare Earth: Why Complex Life Is Uncommon in the Universe*, Springer-Verlag, New York.

Address reprint requests to:
Andrew J. Watson
School of Environmental Science
University of East Anglia
Norwich NR4 7TJ, UK

E-mail: a.watson@uea.ac.uk