Evolution of Coding Organisms in Stochastic Radiation Environments

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Stochastic Radiation Environments
Evolution of Coding Organisms in
Evolution (selective or neutral) is driven by genomic diversity, which is produced by mutation (+lateral transfer +gene dupl. +meiosis). Mutation = DNA damage followed by error-prone repair. DNA repair following radiation damage is a major source of mutagenesis even on the current well-protected and quiescently-located Earth. Much other DNA damage is either not repaired (death), or is repaired precisely (no mutation).

Many evolutionary milestones may have been responses to the radiation environment or elaborations of ancient DNA repair pathways. Example: mechanisms involved in lateral gene transfer and meiosis (e.g. homologous recombination during conjugation) are often the same as DNA repair pathways.

Ionizing radiation (e.g. Micahod & Wojcieszakowska 1994).
Early terrestrial organisms were exposed to substantial UV radiation.

Archaea, ≈ 2.8 to 3.0 Gyr ago, and perhaps much earlier.

- Obligately and facultatively anaerobic bacteria show intrinsic resistance to UV damage and use photoreactivation DNA repair.

- Gene sequencing of major bacterial families (Xiong et al., 1999) and analyses of bacterial biomarkers (Brock et al., 1999) suggest anaerobic photosynthesis arose by mid-2Gya.

- Possibly 3.5 Gyr ago (Schopf, 1993, Rossignol, 1999).

- Possibly 2.7 Gyr ago (Rye & Holland, 2000).

- Evidence for land-dwelling microbes at least as early as cyanobacteria.

- Complex DNA repair pathways.

- "Deep-branched" prokaryotes possess well-developed photoreactivation DNA repair.

- UV exposure > 2Gya.

- Obligate and facultatively anaerobic bacteria show intrinsic resistance to UV damage and use phytochrome.
Over long timescales, the radiation environment anywhere in our Galaxy is almost certainly highly stochastic:
Would enhanced and stochastic irradiation/mutation rate prevent/sterilize life, or instead accelerate its occurrence and evolution?

- In vitro and artificial life evolution: enhanced and stochastic irradiation/mutation rate

- Production of biological precursor molecules: Much of the radiation is easily form H₂CO (Kasting 1993) and HCN, important precursors to amino acids and nucleotide syntheses (Adami et al. 2000 and refs.). Mutations that increase photolysis thresholds for H₂O, CO₂, and N₂ can more easily form organic molecules. Flares and other stochastic radiation events provide a wide information channel on which natural selection can operate. Mutations that increase fitness can be regarded as random mutations, that increase environment-enriched environments (e.g., Adami et al. 2000 and refs.).

- Neural network/genetic algorithm learning: more efficient in the presence of bursts of strong mutation (Montay & Mcilvain, 1997).

Critical fluences for ionizing radiation (simplified)

- Critical fluences reach organisms.
- All ionizing radiation (x-ray, γ-ray, cosmic rays) important if sufficient molecular nodes of interest.
- Wave lengths
  - UV between 200 nm ~ 300 nm for terrestrial DNA damage/mutation at ~300 nm for solar spectrum (for terrestrial UV)
  - 0.7% and C(2) “edges” and 300-350 nm (peak
  - Ozone layer: to reduce O³ by ~30-40% requires ~10⁸-10⁹ erg cm⁻²
  - Viruses.
  - Prokaryotes: Huge range of lethal doses, from ~10 Gy (e.g. halophile Vibrio parahaemolyticus) to 500-1000 Gy (D. radiouss spores, some
  - Many eukaryotes: F_{G11} ~ 5 x 10⁷ erg cm⁻² (1 Gray in water or air)
  - Generalization: easier to mutate or sterilize organisms than to alter atmospheric chemistry.
  - Gehrels et al. 2002)
Critical fluences for UV (cont'd)

Best-studied prokaryotic systems (E. coli, B. subtilis) have mutation doubling dose could be much smaller than lethal dose. (D. rad ~ 100 times larger lethal dose.)

Variation, both smaller (e.g., Asad et al. 2000) and larger F_{cr} ~ 10^4 erg cm^{-2} for lethality (wild types). Some Best-studied prokaryotic systems (E. coli, B. subtilis) have much larger lethal doses.

For details, nucleotide excision repair -- Scalzo, Williams, Wheeler 2002
Potential evolutionary effects:

- Burst of hypermutation: generally lethal to exposed population if mutation rate is already optimized to maximize diversity without resulting in selection pressures. However, it can provide more diversity for selection (cf. unknown status of “mutator genes” which enhance mutation rate).

- Evolution through alteration of atmospheric chemistry:
  
  Duration of event must be much longer than relaxation time of organisms (in case of atmospheric and fixation time of organisms). This allows for adaptive mutations to spread through the population.

- Other environmental alterations:
  
  Examples include ice sheet sublimation, cloud cover fluctuations, and atmospheric chemistry changes, which provide opportunities for evolution and speciation.

- But part of hypermutation could be beneficial by altering ecological connections and niche structure.

- This partial sterilization will drive evolution toward maximized diversity without resulting in “mutational meltdown.” This catastrophic sterilization will drive evolution toward increased diversity, and if mutation rate is already optimized to
  
  generally lethal to exposed population.
Potential evolutionary effects (con’t):

- Development of radiation resistance among survivors? In vitro experiments (esp. Ewing 1995, 1997) and theory suggest all three results more-or-less continuous (until stellar activity dies down in billions of years).

Frequent flares on dMe parent stars may give all three results more-or-less continuous.

- Cosmic rays from supernova could be most likely event for disruption of atmospheric chemistry (and development of radiation resistance in longer-lived organisms), because scattering off interstellar magnetic fields fluctuations results in large spread in cosmic ray arrival times (Shklovsky & Sagan 1966). However, frequency of such events is very uncertain.

- Cosmic rays from supernovae qualify. Very uncertain. SNe and UV from novae may not. UV and γ-rays from weeks for E. coli – like generation time (~1 hr). UV and γ-rays from long-lives. For E. coli, it is ρm – like generation time (1–2 generations) during the time of enhanced radiation environment. Fixation of mutation in population during the time of enhanced radiation environment (depending on population size). Fixation of mutation in long-lives must be greater than a few hundred generations (esp. Ewing 1995, 1997) and theory suggests that duration of experiments (esp. Ewing 1995, 1997) and theory suggests that duration.
Estimating the recurrence time for significant astronomical events

In two-dimensional geometry (gamma-ray bursts):

\[ T = \frac{4 \pi F_{\text{source}} A}{E_{\text{source}}} \]

Where:
- \( E_{\text{source}} \) = energy of event (ergs),
- \( S_{\text{source}} \) = Galactic rate of sources.

But for supernovae, UV radiation, must correct for vertical Galactic structure and dust extinction (see next figure).

In three-dimensional geometry (supernovae, novae, etc.):

\[ T = \frac{6 \pi^{1/2}}{S_{\text{source}}} \left( \frac{F_{\text{source}} A}{E_{\text{source}}} \right)^{3/2} \]

Where:
- \( E_{\text{source}} \) = energy of event (ergs),
- \( S_{\text{source}} \) = Galactic rate of sources.

But for supernovae UV radiation, must correct for vertical Galactic structure and dust extinction (see next figure).

Separate calculation:

Radiative transfer through the planetary atmosphere (from events per unit volume. Attenuation factor \( A \) corrects for events). Where:
- \( E_{\text{source}} \) = energy of event (ergs),
- \( S_{\text{source}} \) = Galactic rate of source.

Average time between events of some type producing critical fluence...
Recurrence time for UV supernova events of a given fluence for a planet with no ozone shield at a typical position in the Galaxy, including vertical Galactic structure (orange) and interstellar extinction (green).

Recurrence time for UV supernova events of a given received fluence for
For ionizing radiation (x-rays, gammas) the major question is: How much gets to the chemically sensitive altitudes of the atmosphere and to the ground?

Answer: Much more than you'd think! Results of Monte-Carlo radiative transfer calculations (for exponentially attenuated x-rays) show that much gets to the chemically or biologically relevant radiation (100 to 300 nm for UV) is chemically or biologically relevant radiation, with energy losses to the ground as of order 1 percent. Without secondary x-ray redistribution, the fraction of incident energy that gets to the ground as chemically or biologically relevant radiation (100 to 300 nm) is of order 1 percent. The fraction of incident energy that gets to the ground as chemically or biologically relevant radiation is of order 1 percent! Without secondary x-ray redistribution, would only get ~10^{-4} to 10^{-10} percent.

Main result: Even for atmosphere thick enough to support liquid oceans (~500 g cm^{-2}) the fraction of incident energy that gets to the ground as chemically or biologically relevant radiation is of order 1 percent! Without secondary x-ray redistribution, would only get ~10^{-4} to 10^{-10} (depending on energy)!

Next 3 plots illustrate the physics and results.

The ground:

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Radiative transfer of ionizing radiation through atmospheres: high-energy cross sections
Radiative transfer of ionizing radiation: physical processes resulting in x-ray redistribution to UV "bioflux"
Given these modeling results, what are the most significant external (not the parent star) radiation sources? Probably negligible:

- Soft Gamma-Ray Repeaters - energy $10^{43}$ erg, rate (very uncertain) perhaps 1/10 supernova rate.
- External flare stars - frequency enormous, but energy too small ($10^{32} - 10^{35}$ erg).
- Passing OB stars - huge fluence, but negligible flux (see Parravano et al. 2002).

Estimated properties and "significant event" rates in following table.

- Supernova light curve (probably less important than supernovae).
- Gamma-ray bursts - important from anyplace in Galaxy, but short duration, so one hemisphere only?
- Cosmic rays (later arrived, probably diffused) from newly produced radioactive nuclides (mostly $^{56}$Co).

Probable Important:

- Supernovae-hard UV shock breakout, UV from light curve phase, $\approx 10^{43}$ erg.
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- External flare stars - frequency enormous, but energy too small ($10^{33}$ erg).
- Soft Gamma-Ray Repeaters - energy $10^{43}$ erg, rate (very uncertain).

Probable negligible:
But in addition to all these highly intermittent sources, we have overlooked the most obvious fluctuating source of all, one that all planets except rogues will be exposed to: the parent star.

<table>
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<th>Event</th>
<th>Duration</th>
<th>Energy</th>
<th>Rate of Significance</th>
<th>Rate of Galactic Rate</th>
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<td>Planetary cycles (Gyr)</td>
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<td>300</td>
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Astrophysically Significant External Events
Parent star flares may be the most important stochastic radiation source for evolution.

Solar flares: Extrapolate observed hard x-ray frequency distribution (see next plot) to higher energies consistent with historical record, ice-core abundance anomaly interpretations (Stothers 1980), and supernovae next plot to higher energies—consistent with historical record, ice-core abundance anomaly interpretations (Stothers 1980).

Between flares of fluence $F$ at 1 AU is resulting average time $T \approx 100 \frac{F^{1.6}}{10^6 \text{ erg cm}^{-2} \text{ s}^{-1}} \text{ yr}$

And note that the Sun was almost certainly much more active (x-ray, varying much more rapidly).

$T_{\text{rad.}}$ of an Earth-like planet every $\sim 10^6 \text{ yr}$! Mutation rate must be sufficient for severe atmospheric heating, ionization, chemistry, ice sublimation, and lethality to any exposed organisms (including $D$. rad.) of an Earth-like planet every $\sim 10^6 \text{ yr}$!

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How about lower-mass parent stars?
Solar flare frequency distribution: $f(E) \sim E^{-1.6}$

Robust result: frequency distribution $f(E) \sim E^{-1.6}$

Solar flare frequency distribution: EUV to hard x-ray

EUV: Krucker & Benz (1998), Parnell & Jupp (1998b, 1999, 2001), and even radio bursts (Nita et al., 2001), and

Key data: Crosby et al. (2001), agrees with deca-

Hard x-ray: Crosby et al. (1998a), see also Pearce et al. (1998a). Agree with deca-


(EUV): Krucker & Benz

ASchwannen et al.
Flare irradiation of habitable zone planets orbiting very low-mass stars

Low-mass stars (spectral type M, masses below ~0.7 solar masses) spend their first few Gyr as dMe flare stars, and only gradually decline in activity. Since lowest mass stars are most common in the Galaxy, and 3D hydro/climate simulations by Joshii et al. (1997) showed that atmospheres thicker than about 30 mb, low-mass stars should be the most common site for habitable planets. Atmospheric retention will occur in synchronously rotating planets for x-ray fluxes and fluences of order $10^6 - 10^7$ times larger than on Earth once per 100 hours (or so). Above-atmosphere x-ray fluxes and fluences of order $10^6 - 10^7$ times larger than on Earth once per 100 hours (or so).

Flare rate as function of flare energy in U band. Known for about 30 dMe stars, consistent with scaled-up Sun: more frequent, more intense radiation environment.

Habitable planets? Since lowest mass stars are most common in the Galaxy, very low-mass stars (spectral type M, masses below ~0.7 solar masses) spend their first few Gyr as dMe flare stars, and only gradually decline in activity.

Flare irradiation of habitable zone planets orbiting...
X-ray environment of habitable zone planets around low-mass stars: flares and coronal emission enormous compared to the Earth/Sun (Andreeshchev & Scalo 2002)
UV-habitable zone environment relatively mild except during flares: chemically
biologically significant flares every ~100 hr (dMe stars) to ~1000 yr (Sun).

Andreeshchev & Scalo 2002

\[ \Phi_0 = \frac{L_{\odot}}{L_{\odot}} \]

\[ \Phi_0 = L_{\odot}^{-0.1} \]
The most common extraterrestrial parent star viewed from the conventional habitable zone.
Astrobiologically significant radiation environment has strong fluctuating component, with timescales between significant events ranging from 10^-1000 yr for parent star flares to 10^6-10^9 yr for external Galactic sources.

Efficiency of transmission of high-energy radiation to low altitudes and surface in the form of redistributed UV is surprisingly large (~1% for Earth)

Evolutionary effects could include partial sterilizations, affecting ecological and niche structure, intense but brief mutational cloud cover modulation, affecting UV transmission, environmental alterations (e.g., ice diversification, frequent "jolts" to atmospheric chemical abundances)

Radiation repair pathways; latter could have been template for more complex biological processes (e.g., lateral gene transfer and meiosis).

Summary