Survival without a fittest

Sourendu Gupta, TIFR, Mumbai

August 28, 2003

1. Biodiversity: what it is and how it arises
2. *E. coli*, plasmids and colicins
3. Games and graphs: games, boards and moves
4. Parallel updates: topology and metapopulation dynamics
5. Stochasticity: Coarsening and power laws
6. Future directions

Biodiversity is in the genes

- Economic importance: monoculture of grapes in France lowered biodiversity and allowed Phylloxera to wipe out all grapes.

- Niches are important: persistence of sickle cell anemia in the Ganges delta region may be adaptive response to Malaria.

- Numerically huge: the immune system has developed combinatorial mechanisms to fight infections— implying immense genetic diversity in infectious bacteria.

Only a small fraction of bacteria occurring in nature can be cultivated in the lab. A 30 gm sample of soil from a Norwegian forest is estimated to have 5×10^5 species of bacteria. V. Torsvik, J. Goksoyr and F. L. Daae, *Appl. Envirn. Microbiol.*, 56 (1990) 782.

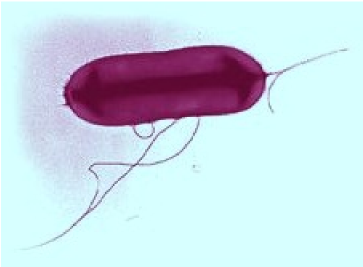
Possible mechanisms

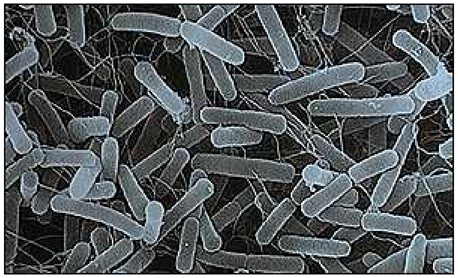
- Stochastic effects such as genetic drift can fix/eliminate genes.
- Many genes are neutral to selection and hence are affected only by drift.
- Even for adaptive genes, some diversity is due to non-equilibrium effects.
- Diversity of ecological niches drive genetic diversity.

This model of bacterial diversity allows a self-consistent description of ecological niches through local diversity of genes and allows quantitative tests of adaptive responses and/or neutrality.

http://www.tomklare.com/

E. coli, **plasmids ...**





Motile, rod shaped bacteria. Natural habitats are soil, water, plants, invertebrates and intestines of most vertebrates. In a normal human organism, prokaryotic cells outnumber human cells by one order of magnitude: of which about 0.1% can be *E. coli*.

Plasmids are loops of DNA which are mobile genes and can shuttle between bacteria. More than 250 plasmids occurring in *E. coli* have been studied—antibiotic resistance, heavy-metal resistance, pathogenicity, metabolic properties, *etc.*. D. L. Hartl and D. E. Dykhuizen *Ann. Rev. Genet.*, 18 (1984) 31.

... and colicins

Colicins are toxins produced by *E. coli* using plasmid DNA. There are more than 30 colicins known. A bacterium producing a toxin but not the corresponding anti-toxin commits hara kiri. Toxin production diverts resources from growth.

For each colicin, one has three variants:

- strain W: the wild type, producing neither the toxin nor the anti-toxin
- strain T: producing both the toxin and the anti-toxin
- strain A: producing only the anti-toxin

The fitnesses are ordered as: $W > A > T > W$. This cyclic fitness pattern has been demonstrated recently. B. Kerr *et al.*, *Nature*, 418 (2002) 171.

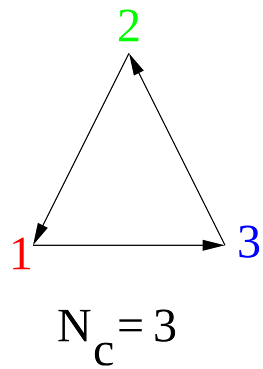

DAD, WHAT CAUSES WIND?
TREES SNEEZING.
REALLY??
NO, BUT THE TRUTH IS MORE COMPLICATED.
DIST BY ASIA FEATURES
THE TREES ARE REALLY SNEEZING TODAY.

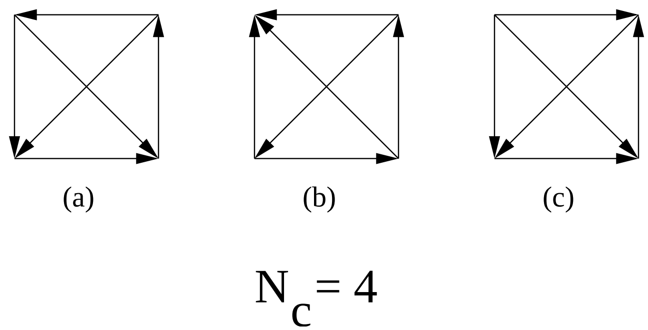
Games and graphs

Analysis using game theoretic models on graphs is a standard technique of modern population biology.

- The evolution of cooperation was investigated in a game-theoretic model in which the Prisoner's dilemma is played repeatedly. Often the Nash equilibrium is avoided, and cooperative strategies spread through a population.
- Evolution of tree heights has been investigated as a game theoretic model in a flat landscape.
- Competition between species of grasses has been investigated as a game on a 2d square lattice.

Dominance Games

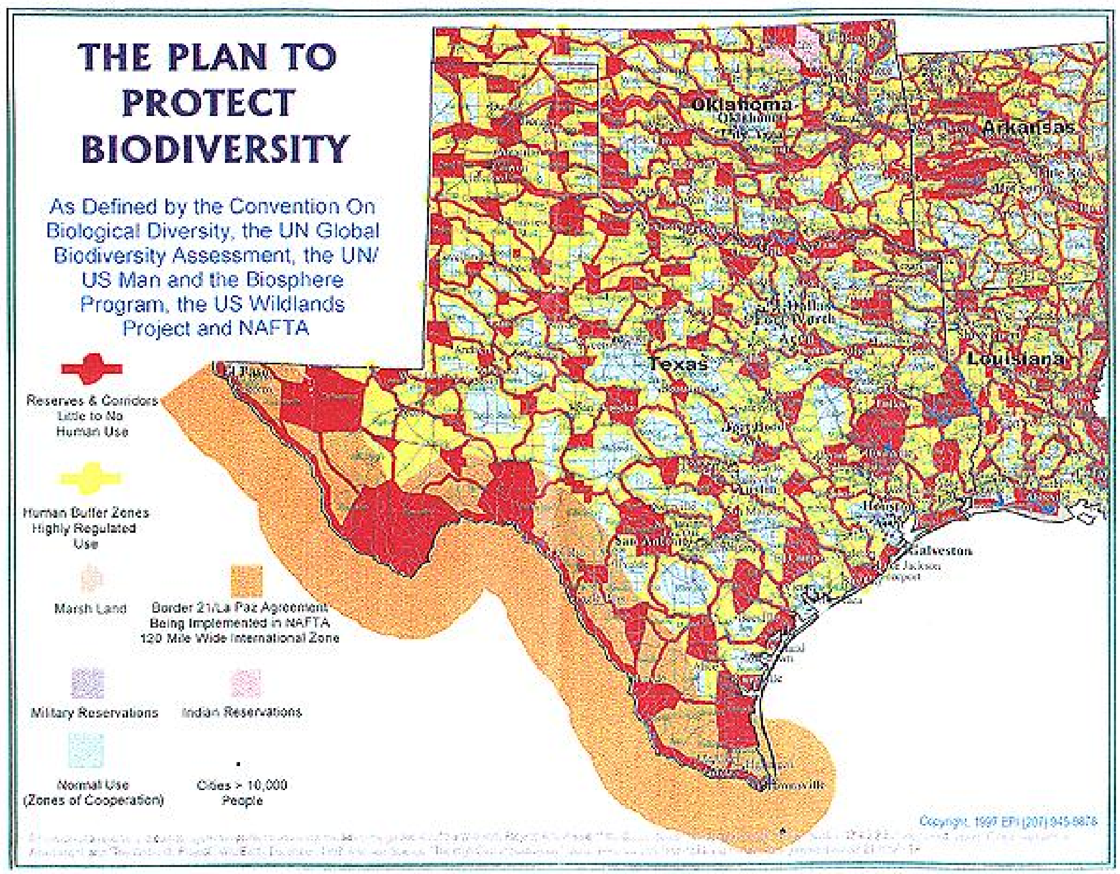




Every game is a matrix or a graph. The 3-color *E. coli* TAW game has the payoff matrix $\begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix}$.

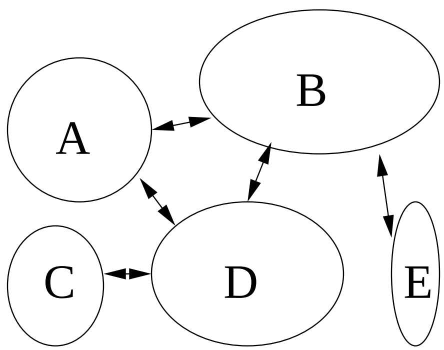
Dominance games are generalizations: define by requiring o arbitrary directed polygons or o a 3 colour dominance sub-game. The second alternative is more stable.

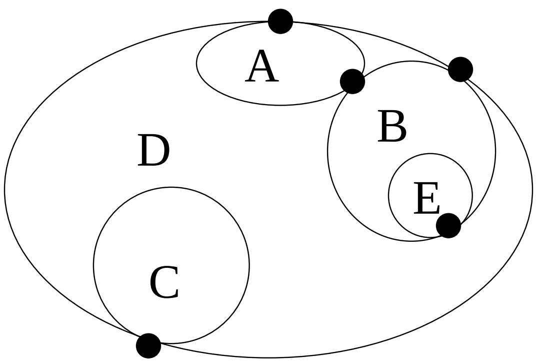
Populations, meta-populations and conservation



Game graphs: the board

I will mainly analyze the game played on a 1d lattice with periodic boundary conditions— a loop of string coated with agar and inoculated with the bacteria.





Then generalize this to a small-world graph built over this by adding some bonds at random: model of metapopulations of *E. coli*.

Updates: the moves

1. Parallel update (PU): all players play a game with each neighbour and assess their winnings at the tick of a clock.

2. Stochastic sequential update (SSU): at the tick of a clock a randomly chosen pair of neighbours plays the game (match time units to PU).

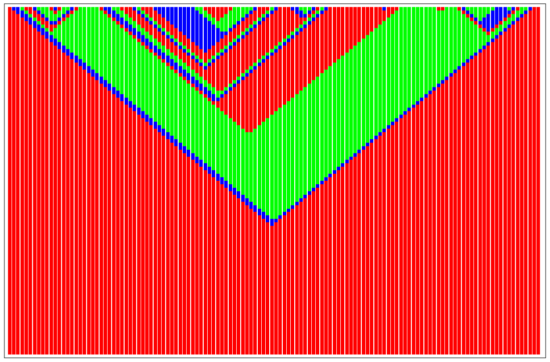
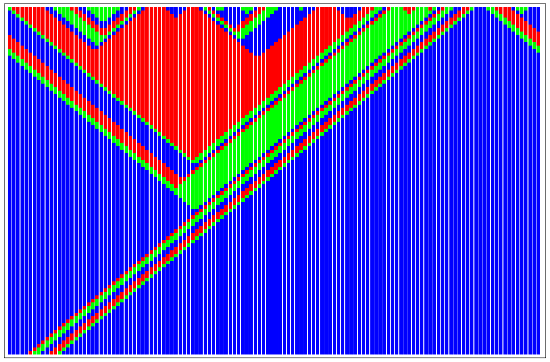
. . .

1. Invasion update: winner takes over the loser's site, play by pairs

2. Nash update: each site taken over by the neighbour with largest winnings.

3. Pareto update: a site taken over by the neighbour with largest winnings only if that site has less than average winnings.

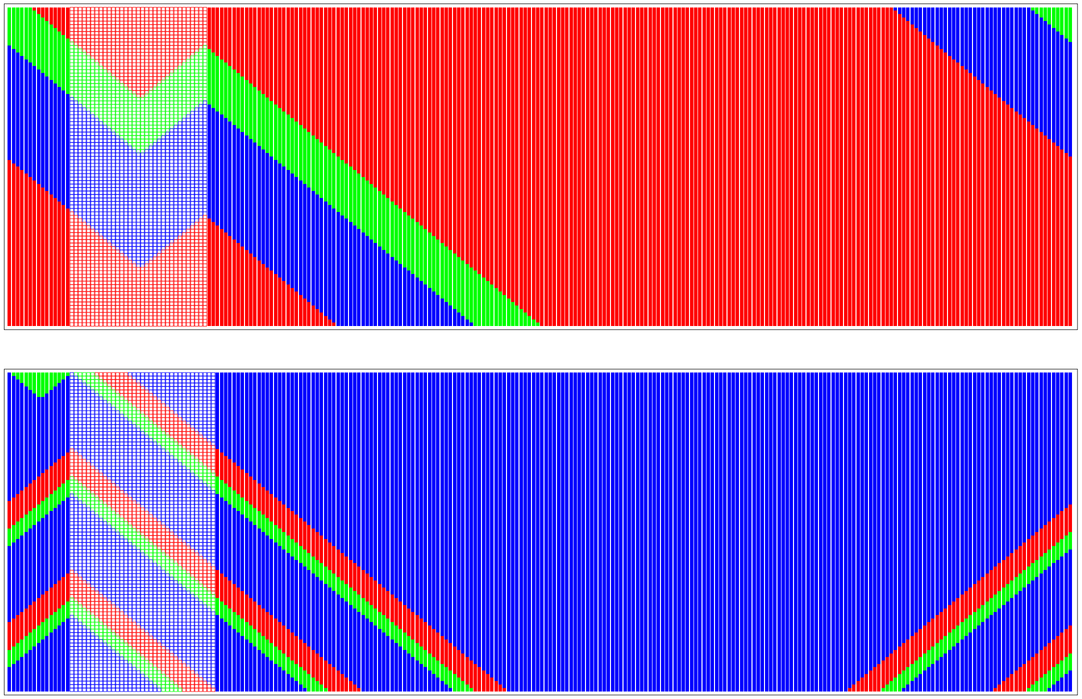
Parallel updates

Choose random initial configuration and evolve: kinematic relativity emerges. Locally stable structures have $\mathrm{lifetime} > \mathrm{size}$. Initialization is a winding of the lattice over the game graph (winding along the arrows gives a right moving interface). Winding number is chirality, χ. Locally stable structures have $\chi \in \{-1, 0, 1\}$.

- Biodiversity lives: χ is conserved.
- Genetic drift is a random walk: $P(\chi = 0) \propto 1/\sqrt{N}$.
- Carrying capacity is zero: $\langle \chi \rangle \propto \sqrt{N}$,

Parallel updates: metapopulation dynamics



Tangled loop: the shortest loop with $\chi \neq 0$ drives the rest. The period is the size of this loop. Lessons for conservation ...

Correlations

$C(r,t;r't')$ = probability that the site r at time t is of the same colour as the site r' at time t'. Translationally invariant for $t,t' > N/2$—

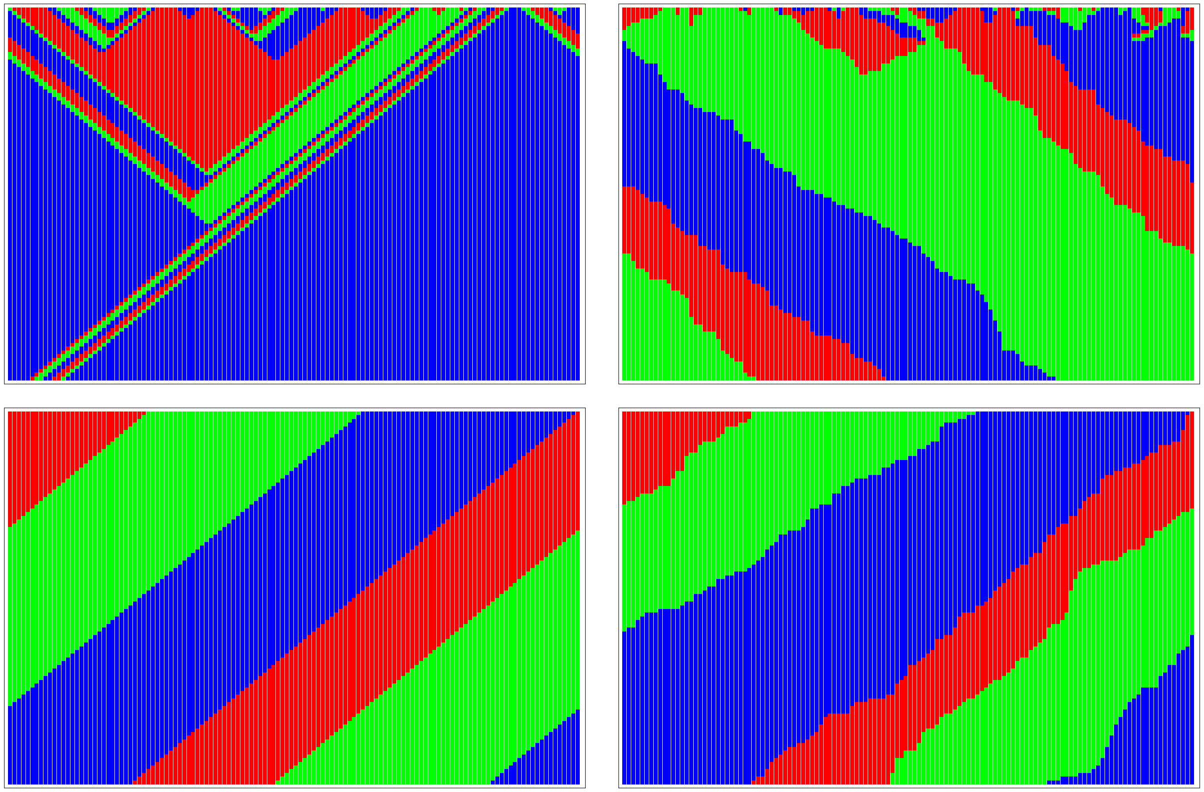
$$C(R+r,T+t;R,T) = C(r,t) = C(|r+\overline{\chi}t|) = \sum_{k=0}^{N-1} c_k \cos\left[\frac{2\pi k}{N}(r+\overline{\chi}t)\right],$$

The fraction of the population inside a patch of size L is specified by averaging C over all N/L patches of size L—

$$f(L) = \overline{\sum_{x=1}^{L} C(x)}.$$

Clearly, $f(L=N) = c_0$. If there is a typical size, ξ, of domains, then only the Fourier modes with $k \gg N/2\pi\xi$ can be large. As a result, $f(L \gg \xi)$ must be nearly constant. ξ can be identified with the correlation length.

Stochastic Sequential Update



Loss of relativity means interfaces can collide. Rules for interface mergers—

$$L + L \to R, \qquad R + R \to L, \qquad R + L \to \varphi.$$

Interfaces decrease— domain coarsening problem.

Biodiversity must die

$$
\begin{aligned}
p &= \text{number of interfaces} \propto N^{\alpha} \\
l &= \text{average size of domains} \propto N^{1-\alpha} \\
w &= \text{prob that a given domain changes by one} = \tfrac{1}{N} \\
\tau &= \text{time for the domain to disappear} \propto l^2/wN = N^{2(1-\alpha)}
\end{aligned}
$$

When $p = \mathcal{O}(1)$ then $\tau = \mathcal{O}(N^2)$

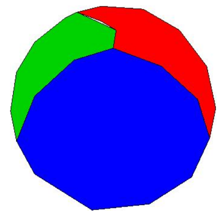
A power law

At time $t \propto N^{\beta} \leq N^{2(1-\alpha)}$, assume $\xi(t) \propto t^{\beta} \propto N^{\Phi}$. Then

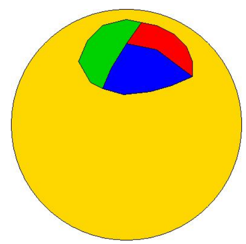
$$C(r,t) = \xi(t)^{\gamma}\mathcal{C}\left[\frac{r}{\xi(t)}\right] = N^{\Gamma}\mathcal{C}\left[\frac{r}{N^{\Phi}}\right].$$

Then $\Phi = 1 - \alpha = -\Gamma$

Future directions



At every triple vertex on a plane, the 3-colour game gives a locally stable structure, and hence gives a stable structure on a sphere.



The non-trivial 4-colour game in 1d has homotopy group Z^3 and hence conserves biodiversity in three basic arrangements. It also gives locally stable structures on a sphere.

Patterns on 2d patches with edges, metapopulations in 2d, scale free networks, dynamic networks, stochasticity ...