The Rise and Fall of Cultures

Modeling the evolution of cultural capacity, and the consequent collapse of populations

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Peter J. Richerson

- The rise of cultures
  - *Environmental Variation and the Evolution of Cultural Capacity*
  - why have some species become cultural and others not?

  Whitehead (2007) *Journal of Theoretical Biology*
- The fall of cultures
  - *The Perils of Cultural Conformism*
  - how does environmental variation and the evolution of culture put populations at risk?
  - Whitehead & Richerson (2009) *Evolution and Human Behavior*

The role of environmental variation

What is Culture?

- *Culture is information or behaviour shared within a population or subpopulation which is acquired from conspecifics through some form of social learning*

Why is culture interesting?

- The second most important form of phenotypic heritability (Maynard-Smith 1989)
  - but transmission and mutation processes and patterns different from genes
  - so cultural evolution may proceed differently from genetic evolution, e.g.
    - Inheritance of acquired variation
    - gene-culture coevolution
    - Group level adaptations
    - ….
  - cultural species are different

U.S. Army website

Why do species differ so much in cultural capacity?

- Most species
  - no evidence of culture
- Some species
  - some evidence of one culturally-determined behaviour (e.g., some songbirds)
- A few species
  - much culturally-determined behavioural variation (e.g., chimpanzees, capuchins)
- A very few species?
  - culture a crucial determinant of behaviour and fitness (some cetaceans, elephants?)
- One species' culture is changing the Earth

The rise of cultures

The Evolution of Cultural Capacity

- The scenario proposed by Boyd & Richerson (1985, ...) and others:
  - in the beginning genes controlled behaviour
  - selection changed population patterns of behaviour
  - but if the environment changes rapidly, phenotypic plasticity is adaptive
  - individual learning is a very effective form of phenotypic plasticity
  - but an expensive form
  - social learning (imitating, etc.) is cheaper, and now selected
  - with behaviour homogenized by social learning, we have *culture*

Environmental change triggers the evolution of:

- Phenotypic plasticity
- Individual learning
- Social learning
- Culture

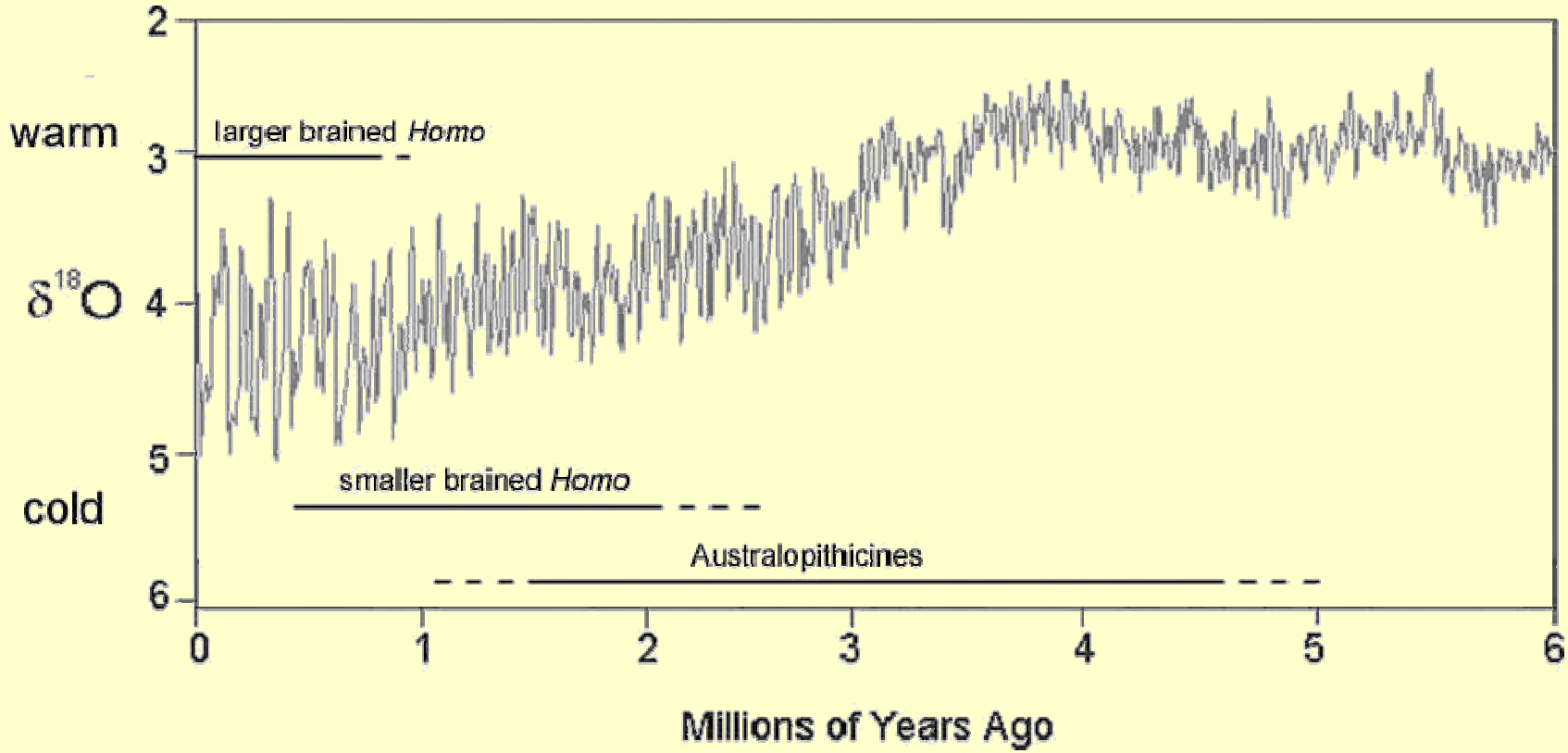
But why in some species and not others?

Maybe differences in the perceived environment

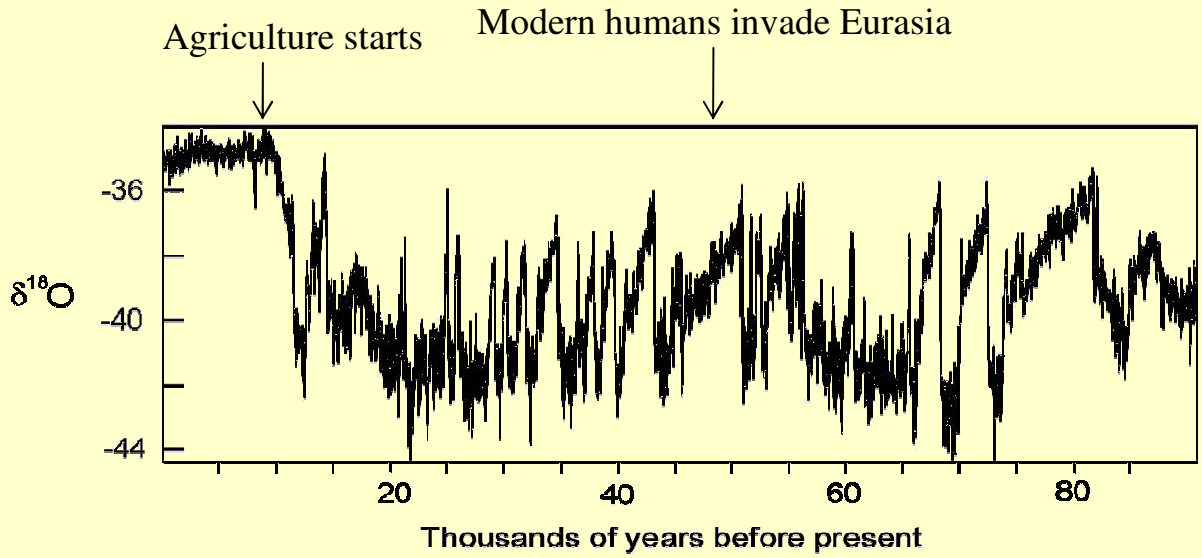
Some suggestions

- Humans developed cultural capacity in Pleistocene as climate became much more variable (Richerson & Boyd 1988; 2004)
- Cetaceans are generally more cultural than terrestrial mammals because the ocean has more low-frequency environmental variation (Rendell & Whitehead 2001)

Pleistocene Climate Deterioration

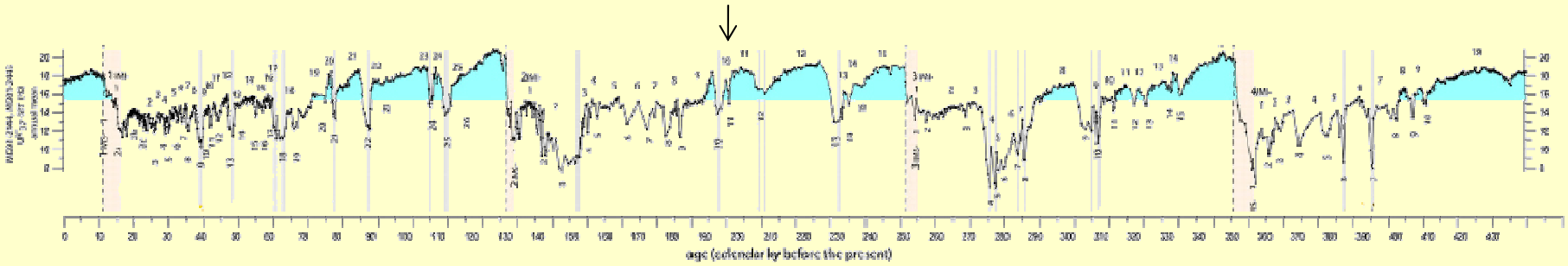


Later Pleistocene



Ditlevsen et al 1996

Biologically modern humans appear



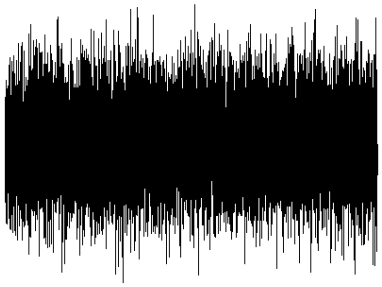
Martrat et al. 2007

Some models:

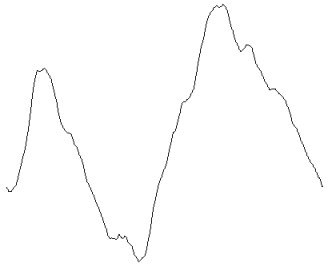
- Patterns of environmental variation should affect the evolution of different modes of behavioral control
  - Boyd & Richerson, 1983, 1985, 1988, 1996
  - Feldman et al., 1996
  - Lachmann & Jablonka, 1996
  - Laland et al., 1996
  - Wakano et al., 2004
  - Aoki et al., 2005
- Analytic models that only looked at small part of range of options

More complete model

- Individually-based, evolutionary, stochastic model
- 15 behavioural control strategies compete against one another
- Environmental variation simulated using *1/f* noise (ω is slope of inverse power-frequency spectrum)



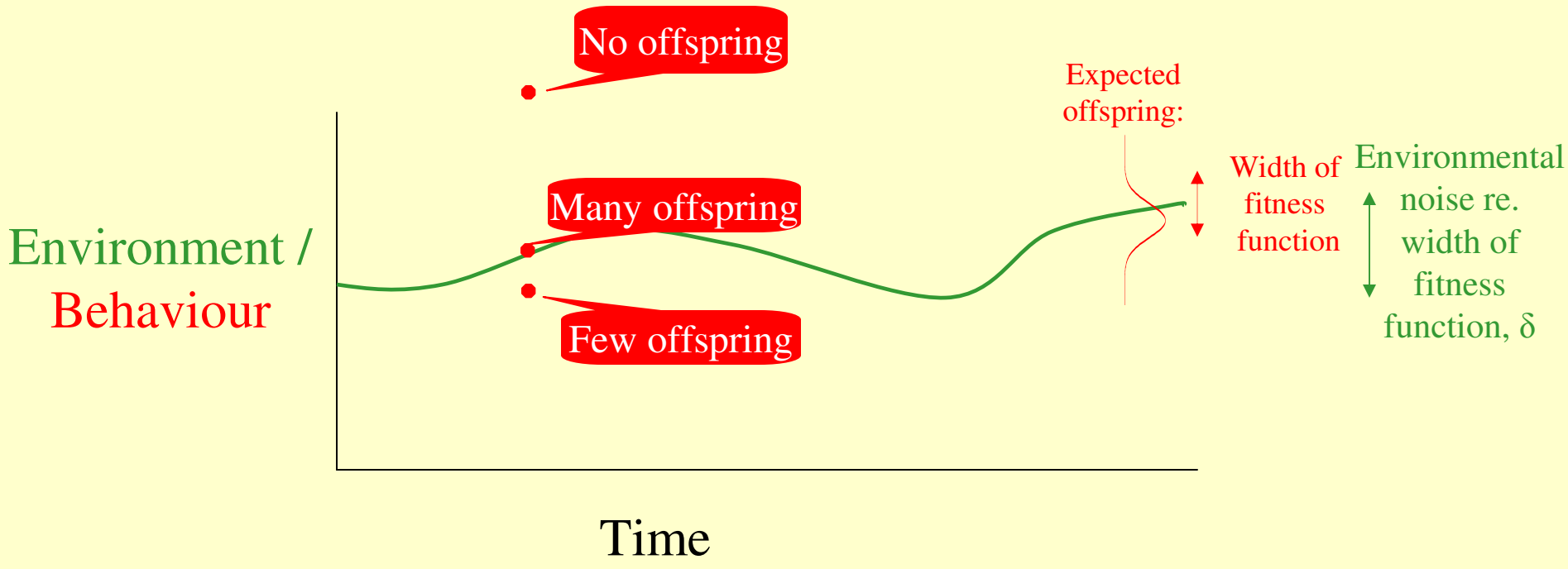
White Noise ω = 0



Red Noise ω=2

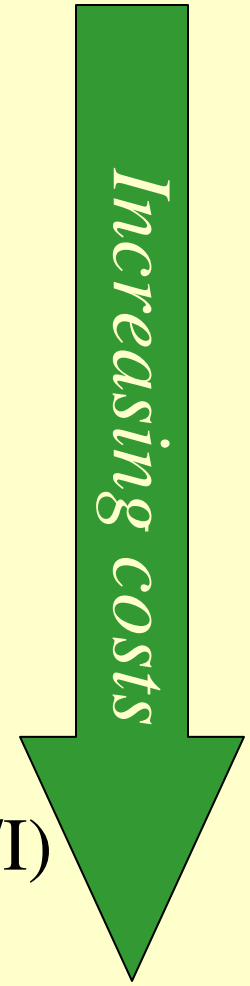
More complete evolutionary model

- Fitness (expected number of offspring) of individual dependent on difference between its behaviour and environmental optimum



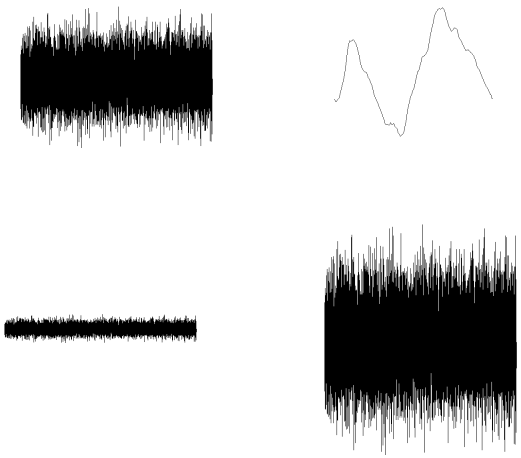
Behavioural control strategies

- Genetic determination (G)
  - *do what your genes (from parent) say + error*
- Vertical social learning (V)
  - *do what your parent did + error*
- Horizontal social learning (H)
  - *do what everyone else just did (mean) + error*
- Individual learning (I)
  - *do what is best in current environment + error*
- 11 contingent strategies (G/V,G/H,…,G/V/H/I)
  - *assess two or more basic strategies*
  - *do that which gives best expected return*



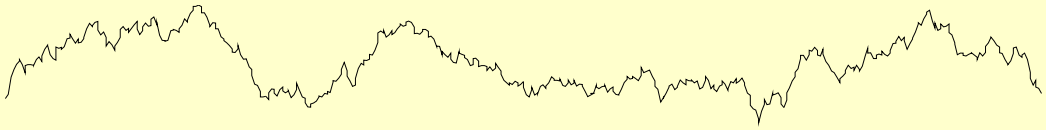
100 model runs with:

- type of environmental noise
  - ω=-0.5, 0.0, 0.5, 1.0, 1.5, 2.0, 2.5
- amount of environmental noise
  - δ=0.125, 0.25, 0.5, 1, 2, 4, 8
- each set with randomly chosen
  - Survival: μ={0.75,0.90,0.95,0.975,0.99}/time unit
  - Behavioral accuracy: σ={0.08,0.15,0.25,0.50,0.75}
  - Cost of vertical learning: C_V=1-{0.01,0.03,0.05,0.07,0.1}
  - Cost of horizontal learning: C_H=C_V-{0.01,0.03,0.05,0.07,0.1}
  - Cost of individual learning: C_I=C_H-{0.01,0.03,0.05,0.07,0.1}
  - Cost of contingency: d={0.90,0.93,0.95,0.97,0.99}



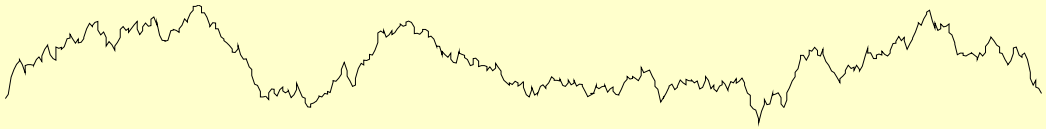
		Time periods			
	1	2	3	4	…
G	100				
V	100				
H	100				
I	100				
G/V	100				
G/H	100				
G/I	100				
V/H	100				
V/I	100				
H/I	100				
G/V/H	100				
G/V/I	100				
G/H/I	100				
V/H/I	100				
G/V/H/I	100				

Environment



		Time periods			
	1	2	3	4	…
G	100	97			
V	100	103			
H	100	88			
I	100	95			
G/V	100	102			
G/H	100	110			
G/I	100	95			
V/H	100	103			
V/I	100	96			
H/I	100	100			
G/V/H	100	100			
G/V/I	100	93			
G/H/I	100	112			
V/H/I	100	113			
G/V/H/I	100	99			

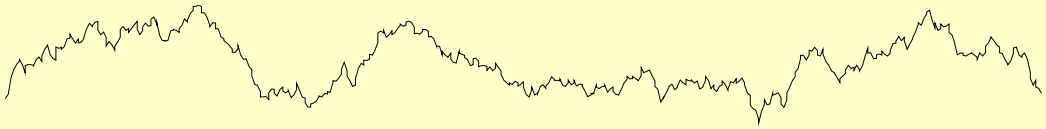
Environment



		Time periods			
	1	2	3	…	138,645
G	100	97			0
V	100	103			0
H	100	88			1,500
I	100	95			0
G/V	100	102			0
G/H	100	110			0
G/I	100	95			0
V/H	100	103			0
V/I	100	96			0
H/I	100	100			0
G/V/H	100	100			0
G/V/I	100	93			0
G/H/I	100	112			0
V/H/I	100	113			0
G/V/H/I	100	99			0

The Winner!

Environment



Some technical details

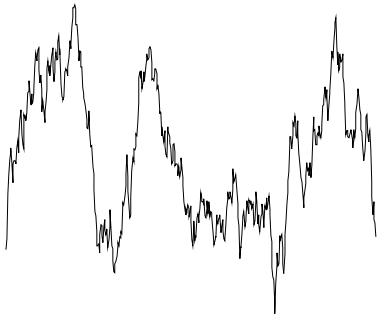
- Programmed in MATLAB
- 1/f noise:

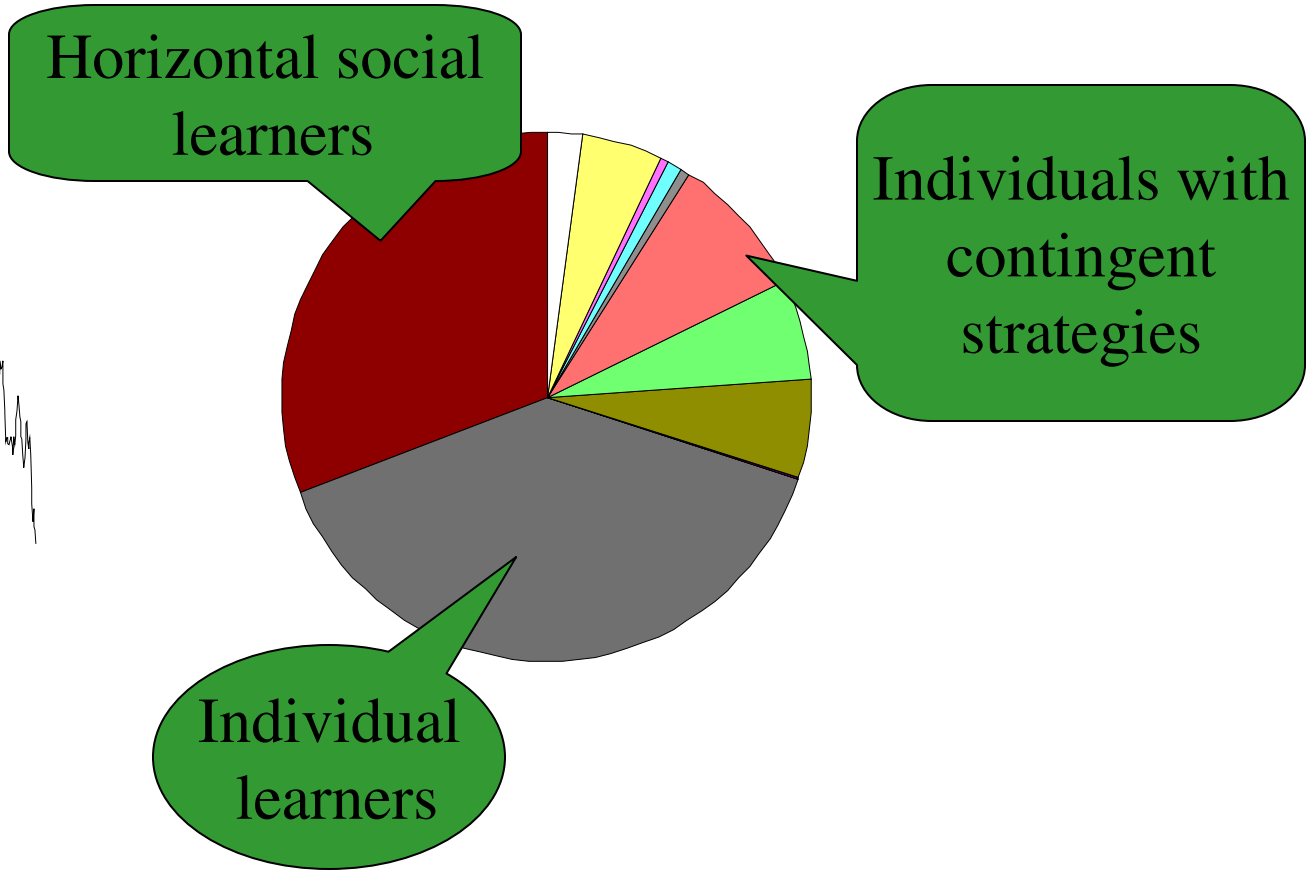
  ifft{(fft(**Y**)$^{-\omega}$} [**Y** is normal random variable, sd δ]
- Number of offspring:

  poissrnd(*w*) [*w* is vector of fitnesses]

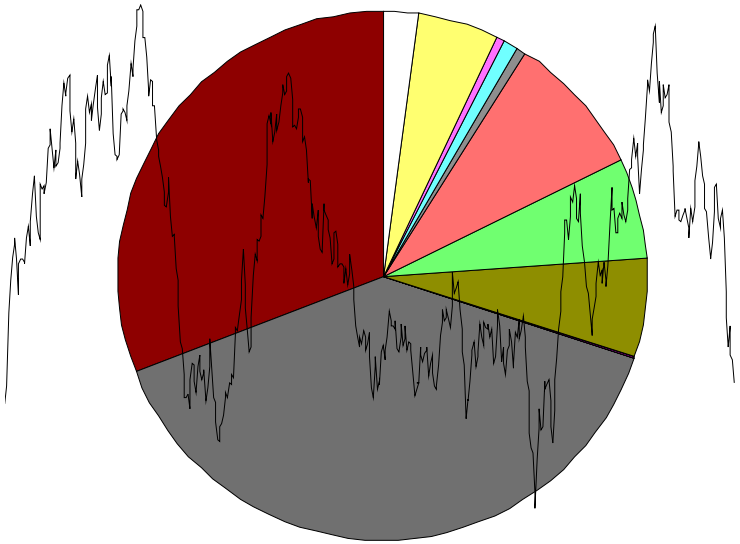
Who is left at end of 100 model runs:

ω=1

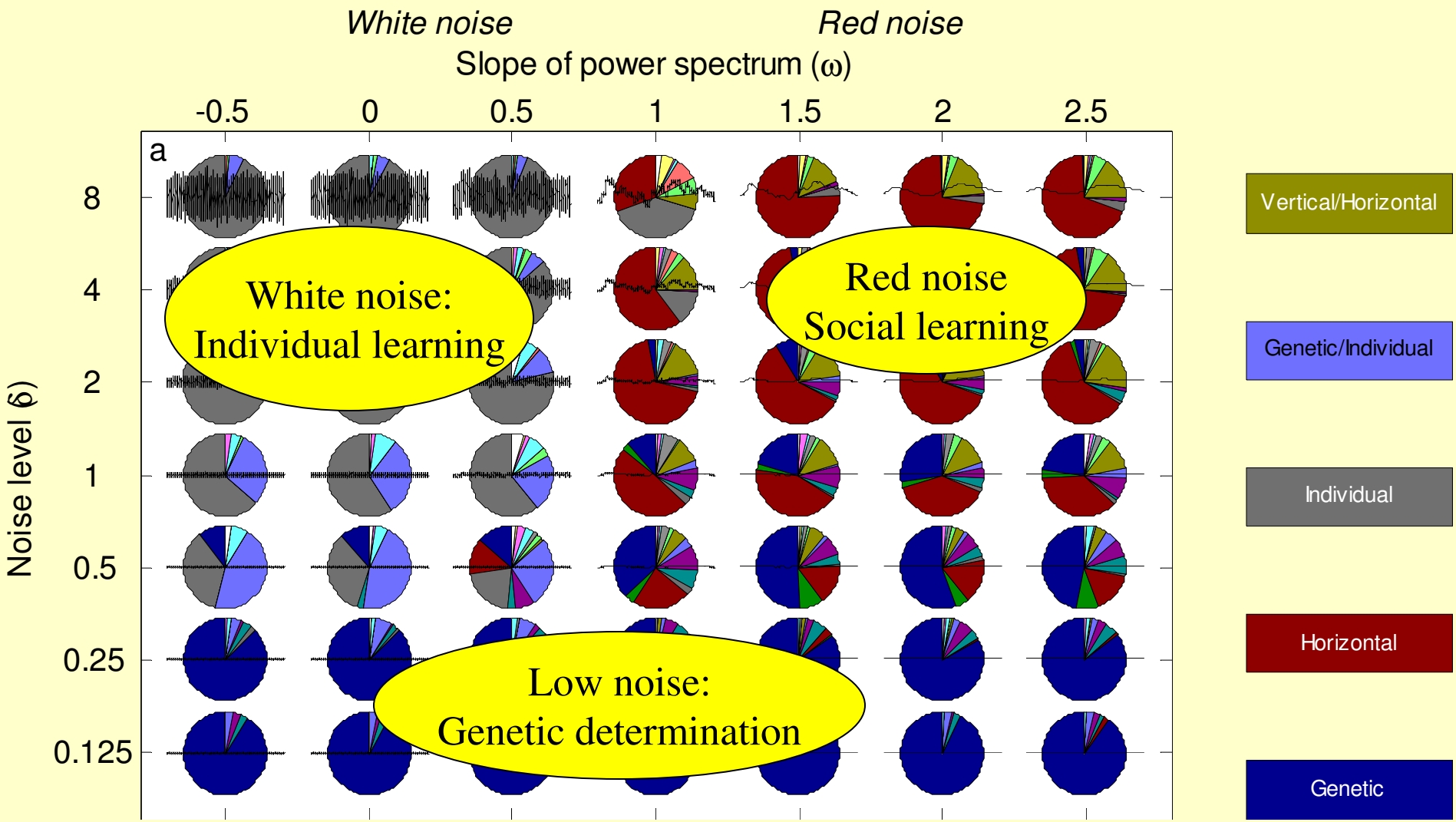




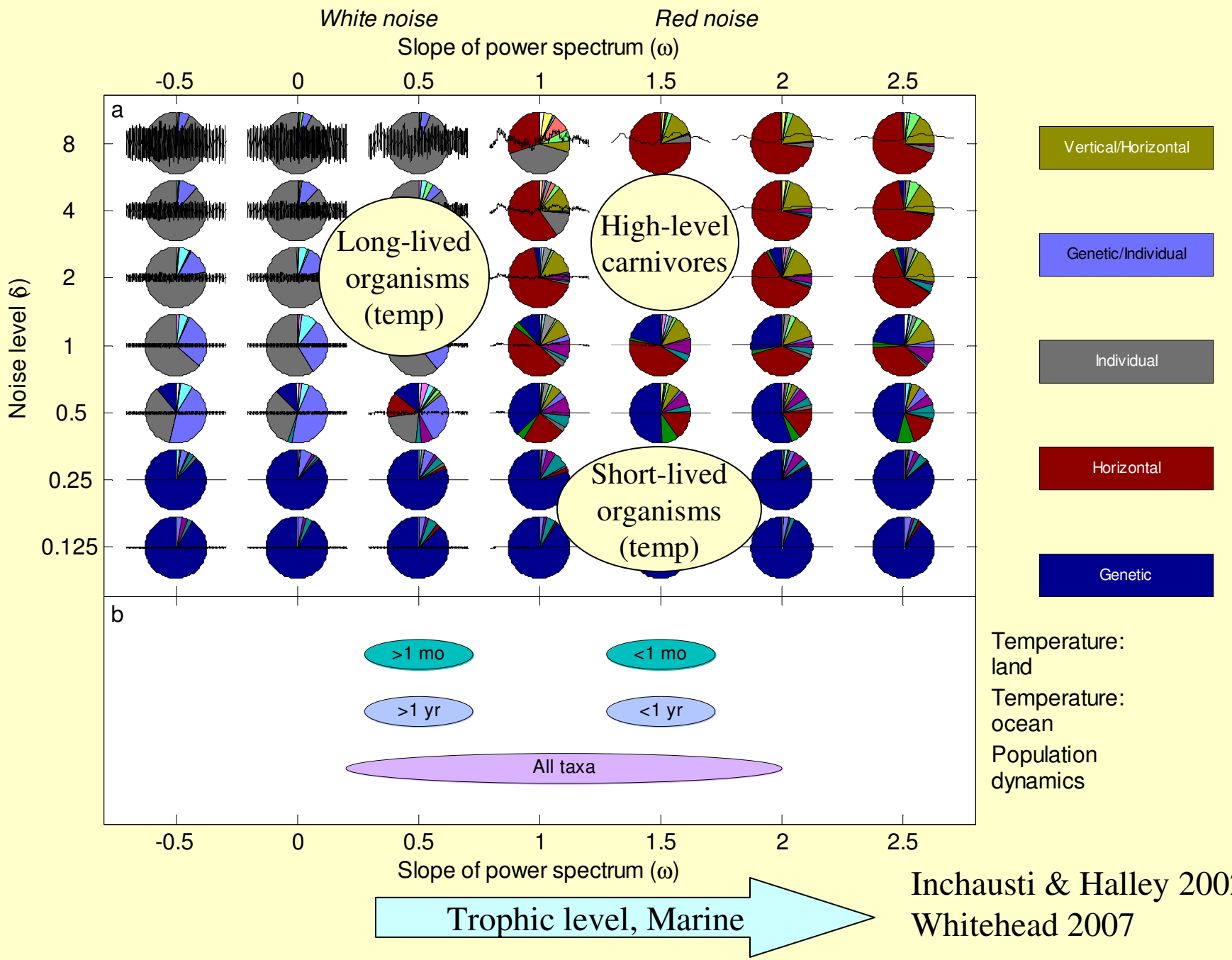
Represent results of runs with particular type of noise as:



So the results are:



Proportion of each strategy remaining
in different environmental conditions for 100 runs



Inchausti & Halley 2002
Whitehead 2007

Conclusion: Evolution of Social Learning and Cultural Capacity

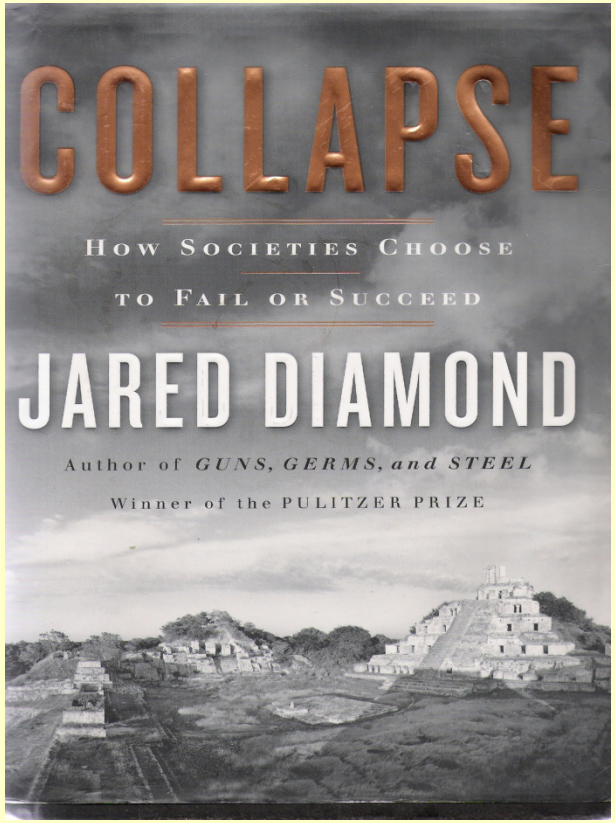
- Learning is more likely to evolve in long-lived animals
- Among long-lived animals, more social learning and culture
  - at higher trophic levels
  - in marine species

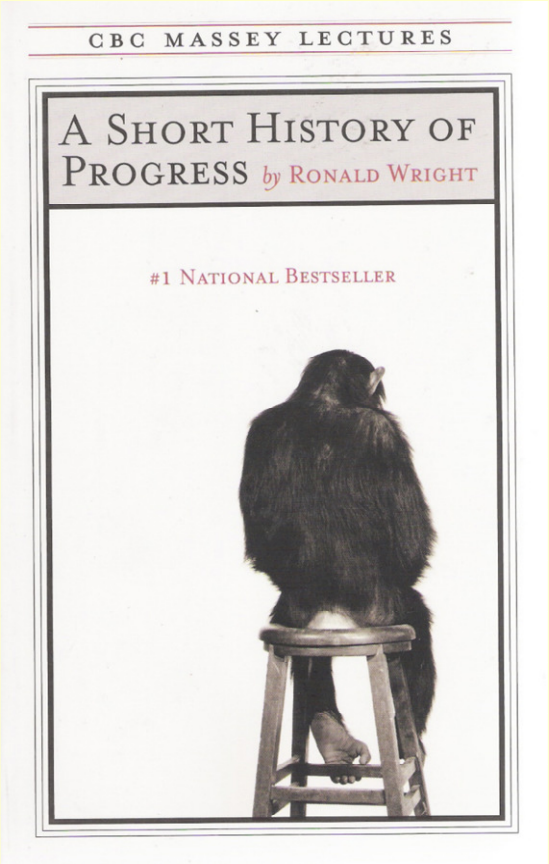
http://animals.timduru.org/dirlist/orca/orca-KillerWhales-15530051.jpg

The Fall of Cultures

the perils of cultural conformism

- How does culture put society at risk?





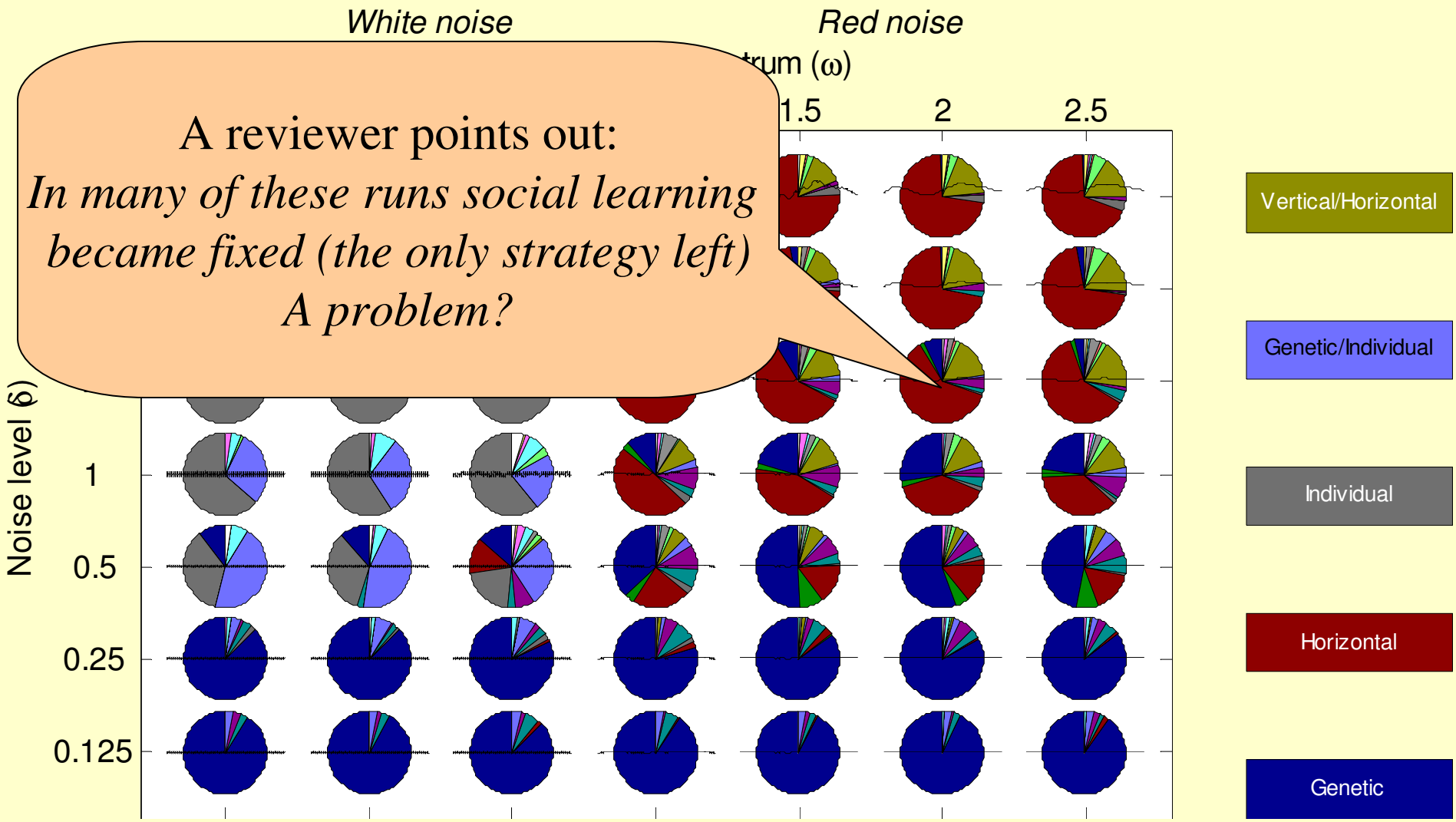
Why do societies fail?

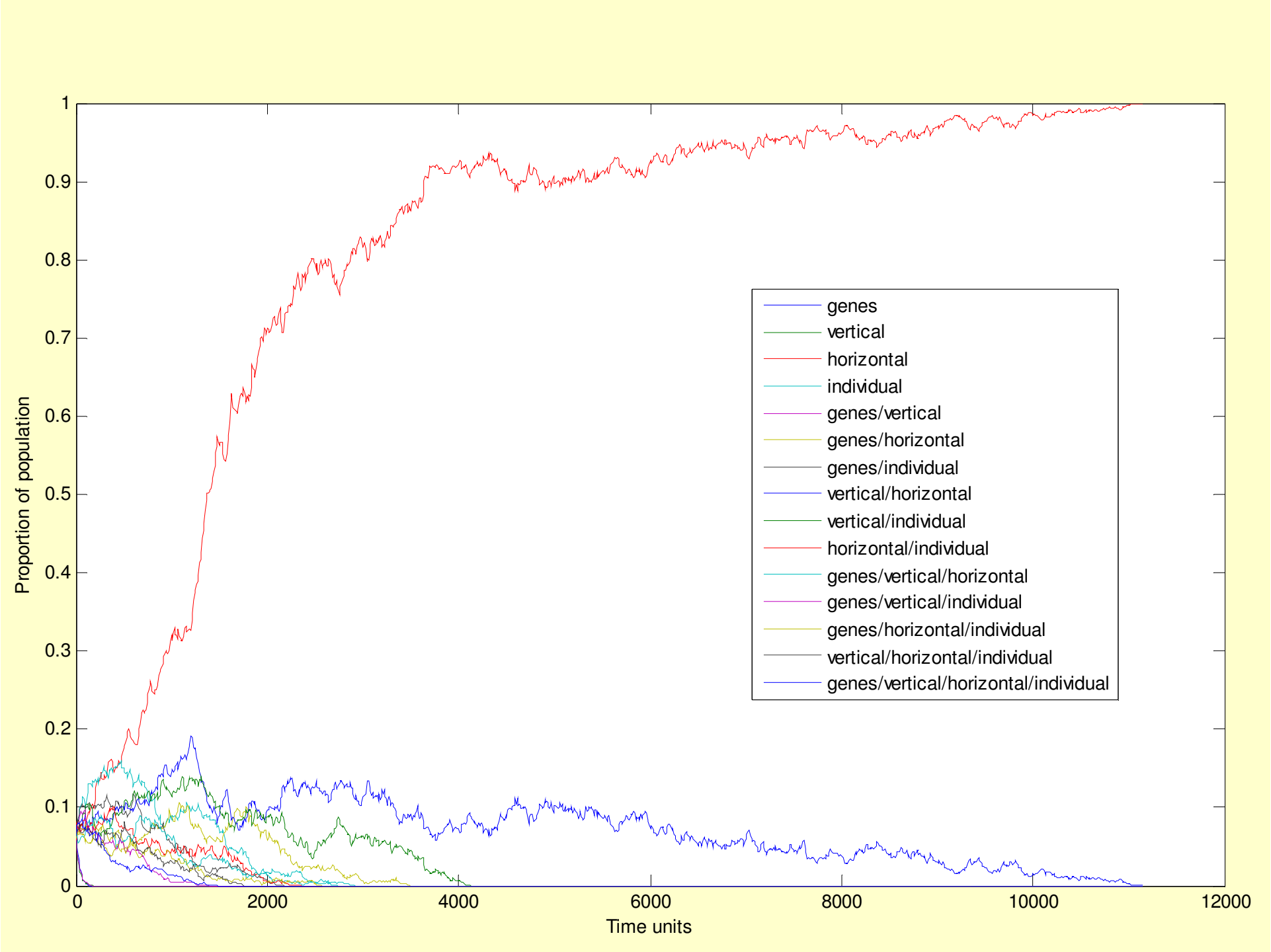
- Competition with other societies?
- Lack of internal coherence?
- *Mismatch of human culture with environment* (Diamond 2005; Wright 2004)

A reviewer points out:

In many of these runs social learning became fixed (the only strategy left)

A problem?




Proportion of population
Time units
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
2000
4000
6000
8000
10000
12000
genes
vertical
horizontal
individual
genes/vertical
genes/horizontal
genes/individual
vertical/horizontal
vertical/individual
horizontal/individual
genes/vertical/horizontal
genes/vertical/individual
genes/horizontal/individual
vertical/horizontal/individual
genes/vertical/horizontal/individual

Previous models (Boyd & Richerson 1985; Feldman et al. 1996; Wakano et al. 2004; Aoki et al. 2005) suggest equilibrium:

- Some social learners, who do better when conditions are stable
- Some individual learners, who do better when environment changes
- If all individual learners
  - social learners can invade
- If all social learners
  - no-one is tracking the environment

Previous models suggest equilibrium:

- Mixed population of social learners and individual learners, *or*
- Mixed, contingent strategy in which individuals can adopt either individual or social learning depending on the circumstances (Boyd & Richerson 1995; Henrich & Boyd 1998)

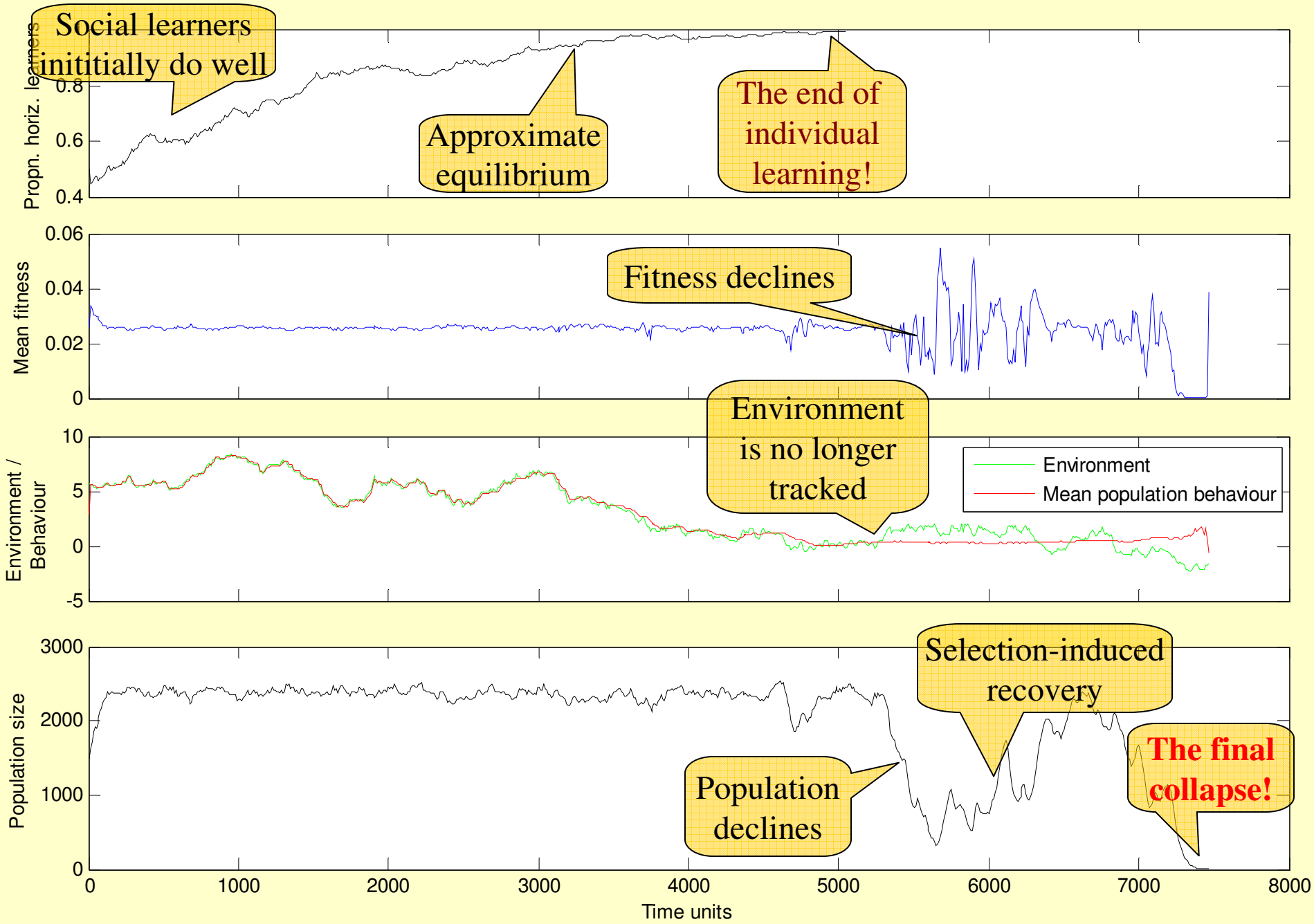
Problems during stable periods?

- Mixed population of social learners and individual learners
  - vulnerable to extirpation of individual learners?
- Mixed, contingent strategy in which individuals can adopt either individual or social social learning depending on the circumstances
  - vulnerable to invasion by pure social learners, and extirpation of mixed strategy?

"Standard" model $\omega=1$

What happens when social learners take over?

- Modify individual-based model to:
  - Just consider individual/horizontal contingent and horizontal social learners
  - Continue beyond fixation


Social learners inititially do well
Approximate equilibrium
The end of individual learning!
Propn. horiz. learners
0.8
0.6
0.4
Fitness declines
Mean fitness
0.06
0.04
0.02
0
Environment is no longer tracked
Environment
Mean population behaviour
Environment / Behaviour
10
5
0
-5
Selection-induced recovery
The final collapse!
Population declines
Population size
3000
2000
1000
0
0
1000
2000
3000
4000
5000
6000
7000
8000
Time units

The “typical” scenario

- Social learning increases
- Contingent individuals (individual learners) are extirpated
  - especially when environment is fairly stable
- Behaviour stops tracking environment
- Fitness declines
- Population collapses and is gone

45/100 runs with standard model parameters

Collapse scenario little changed, or worsened, by:

- High individual learning costs
  - 84/100 runs collapse
- Accurate or inaccurate behaviour (amount of behavioural error)
  - 42/100, 74/100 runs collapse
- Small population size
  - 86/100 runs collapse
- More red (↑ω) or less variable (↓δ) environment
  - 82/100 , 46/100 runs collapse
- Individual learning (rather than contingent), or all 15 strategies available
  - 17/100, 22/100 runs collapse

Collapse generally averted when:

- Low individual learning costs
  - 12/100 runs collapse
- More variable (↑δ) or less red (↓ω) environment
  - 0/100, 0/100 runs collapse
  - Horizontal learning outcompeted by individual learning in very variable or less red environments
- Large population size
  - 5/100 runs collapse
- Vertical rather than horizontal social learning
  - 0/100 runs collapse
  - Vertical social learning outcompeted by individual learning
- Biased horizontal learning (successful, not random, models)
  - 0/100 runs collapse
  - Biased learning allows behaviour to track environment

Collapse

- In real (red; $\omega \sim 1$) environments, during periods of stability, social learners have advantage over individual learners
- Contingent, or individual, learners may be extirpated
- Population collapse likely when society becomes completely culturally conformist
  - individuals do what everyone else does
  - environmental change is not tracked

Evolutionary changes in the behavioral strategies that individuals use to interact with their environment can precipitate *population collapse*

Applicability of model to humans

- Humans do not seem to have fixed, genetically-determined learning strategies (as indicated by model)
- However, learning strategies may be parentally learned (equivalent to genetics)
- And, individual humans have characteristic ways of controlling their behaviour
  - conformist, innovative, …
  - obtained from others (often parents) culturally and, perhaps, genetically
- So maybe model is a reasonable approximation for human behaviour

Real situation for human societies might be worse (1):

- Cultures can stabilize environment (food storage, irrigation, agriculture, …) for long periods, so removing advantages for individual learners
- But, culture can *cause* sudden environmental change
- Methods of stabilizing the environments of individual humans
  - heating, air-conditioning, transport, …
- simultaneously destabilizing the global environment

Real situation for human societies might be worse (2):

- learning strategy might be culturally determined (rather than genetic) increasing conformism: *a culture of conformism*

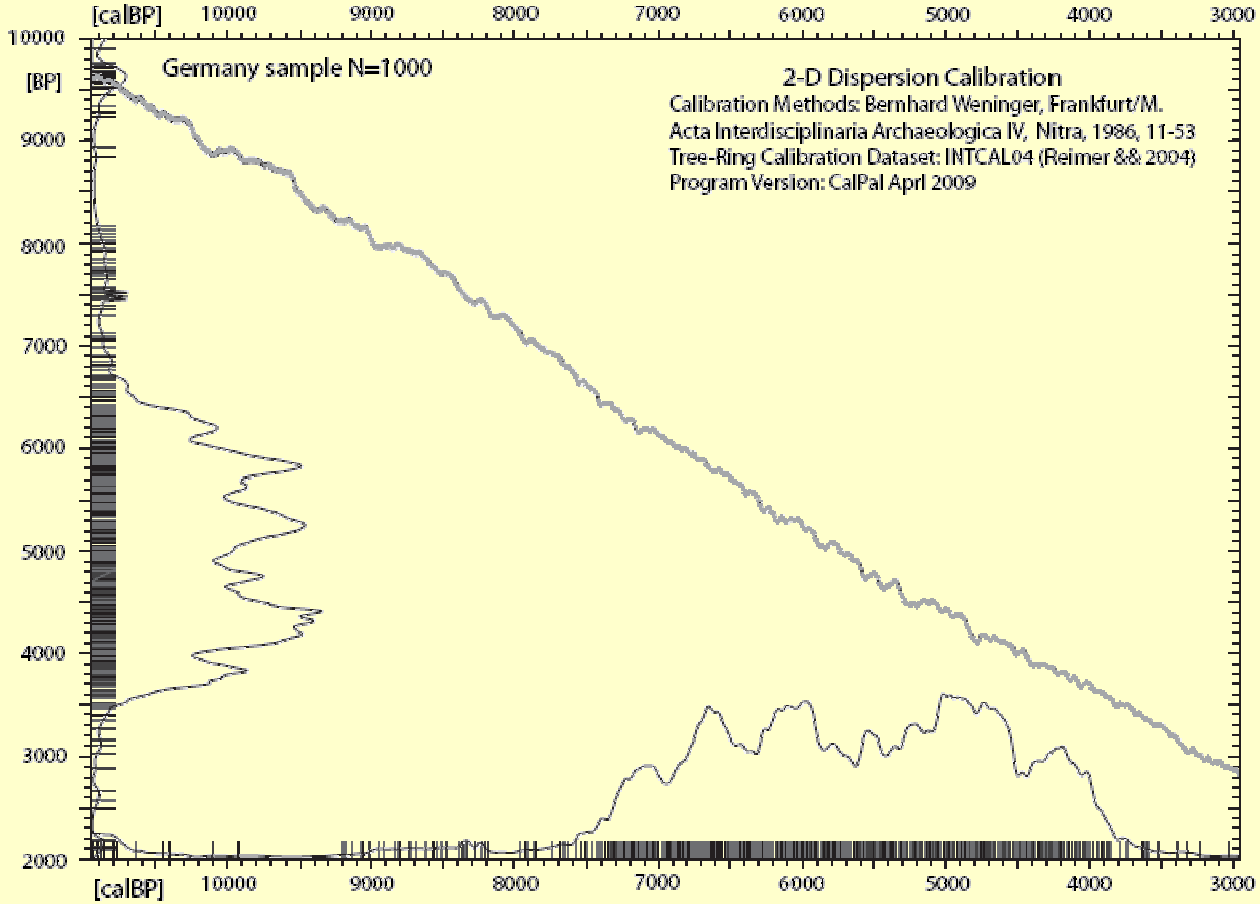
Real collapses

- Greenland Norse
  - driven to extinction (ca. 1,500AD) by cultural conformism (according to Diamond 2005)

http://www.greenland-guide.gl/leif2000/

LBK Culture

(First agriculturalists in Central & Western Europe)



Shennan 2009

Averting collapse

- Increase variability of short-term environment so individual learners have more edge
- Increase parental influence (!)
- Learn from the successful
- Encourage individual learners
  - *be nice to non-conformists*

Summary (1): *The Rise of Culture*

- Learning strategies that are likely to evolve:
  - genetic determination in short-lived, climatically-driven species
  - individual learning in long-lived, climatically-driven species
  - social learning in species whose population biology is dependent on that of other species, especially high-trophic-level marine species

Summary (2): *The Fall of Culture*

- In red environments, horizontal social learning may become ubiquitous replacing individual learning and/or contingent strategies
- With complete conformism the environment is not tracked and the population may collapse
- Such collapses can be averted by:
  - promotion of individual learning
  - learning from the successful

Thanks to

- Andrew Horn, Katie McAuliffe, RAM Myers, Luke Rendell, Tyler Schulz, Rob Boyd
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- NSERC, NSF