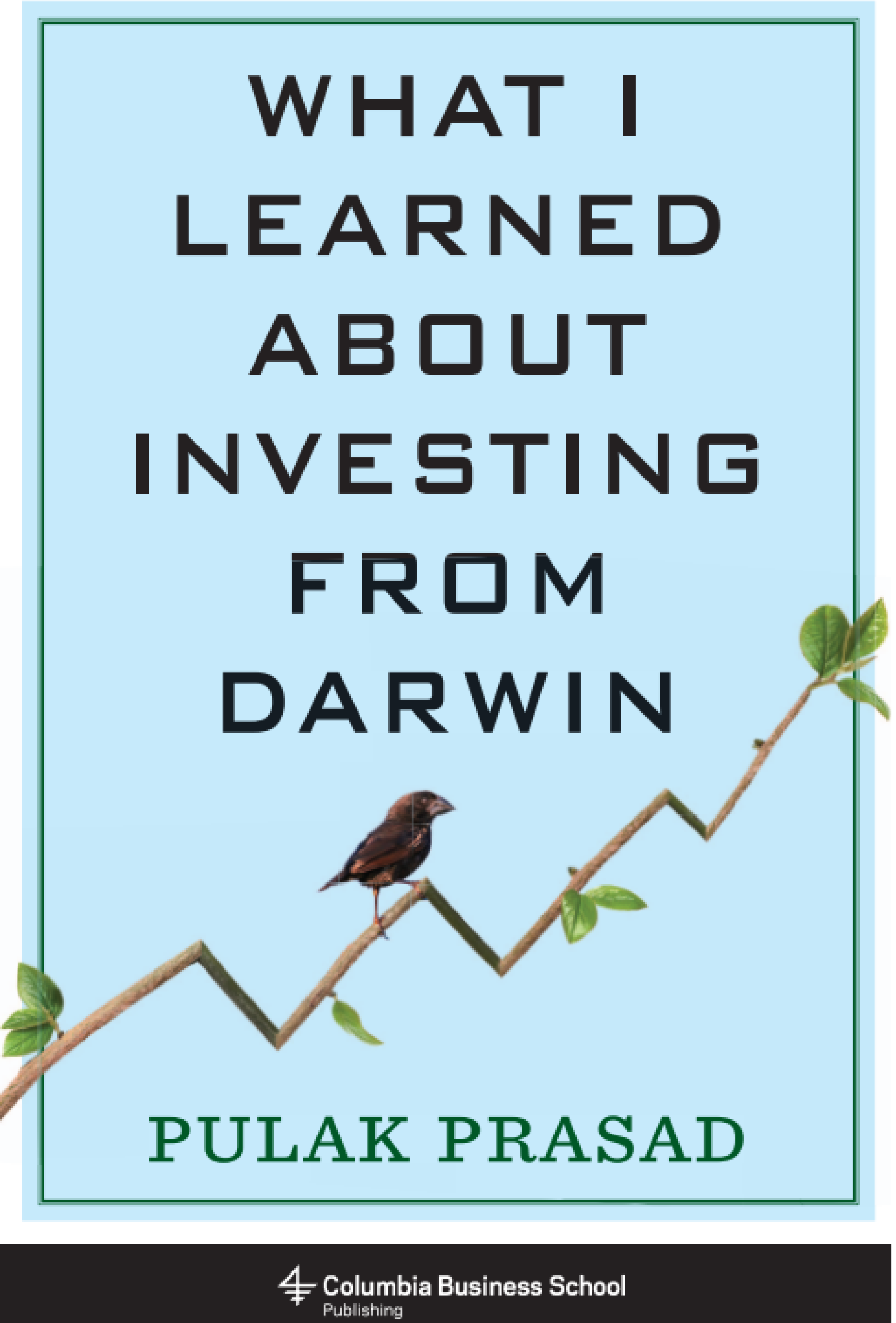
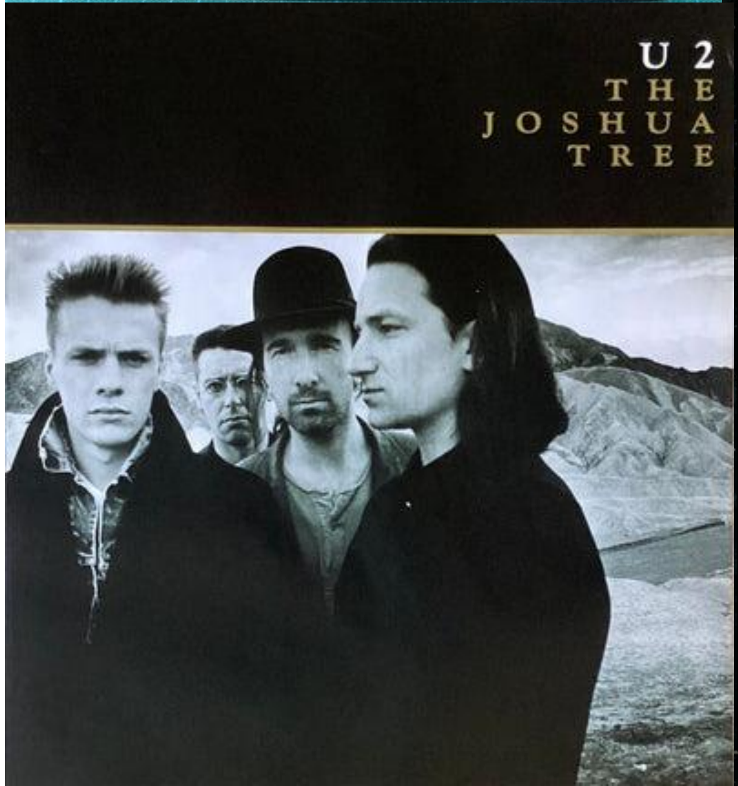
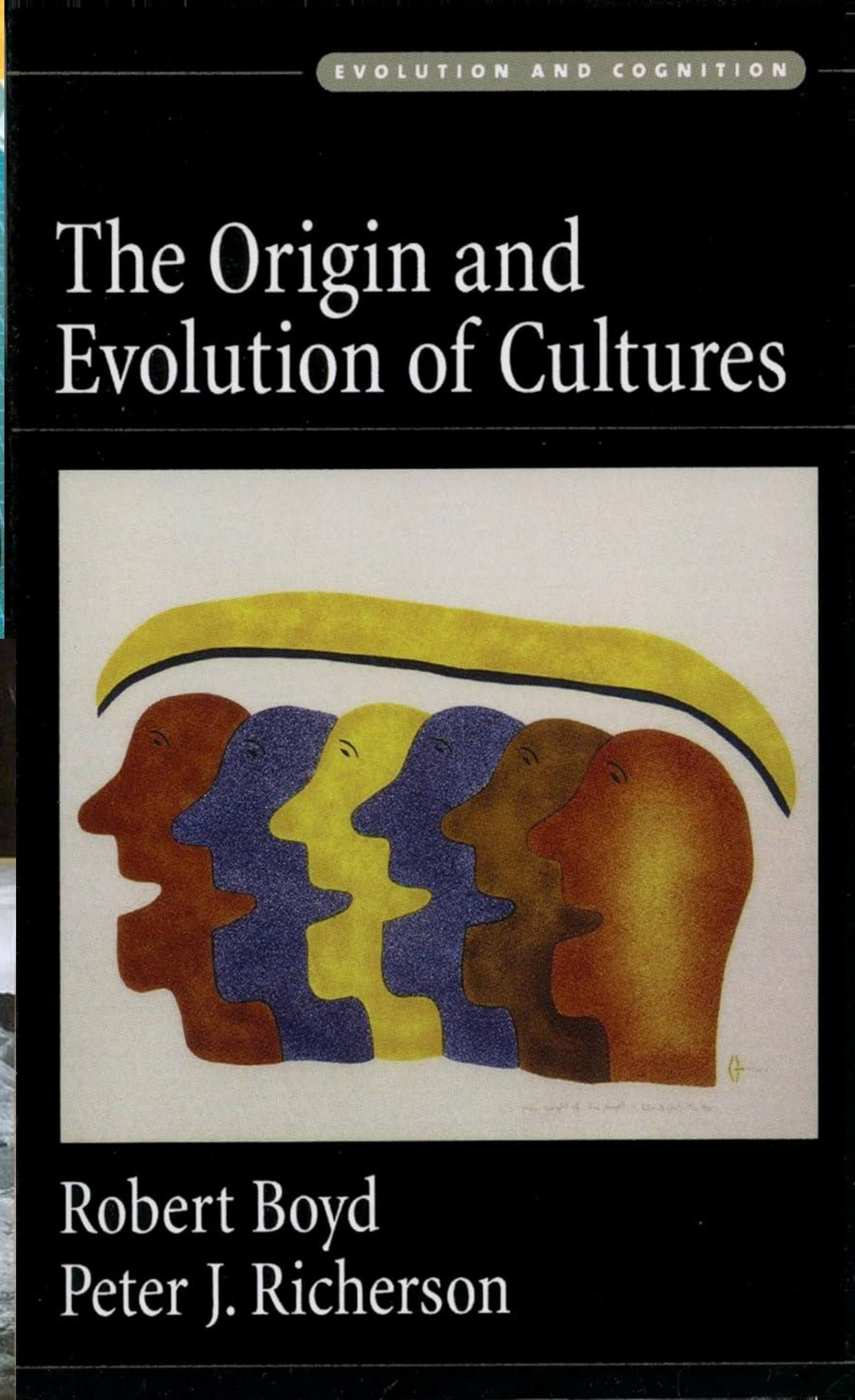

WHAT I
LEARNED
ABOUT
INVESTING
FROM
DARWIN
PULAK PRASAD
Columbia Business School
Publishing

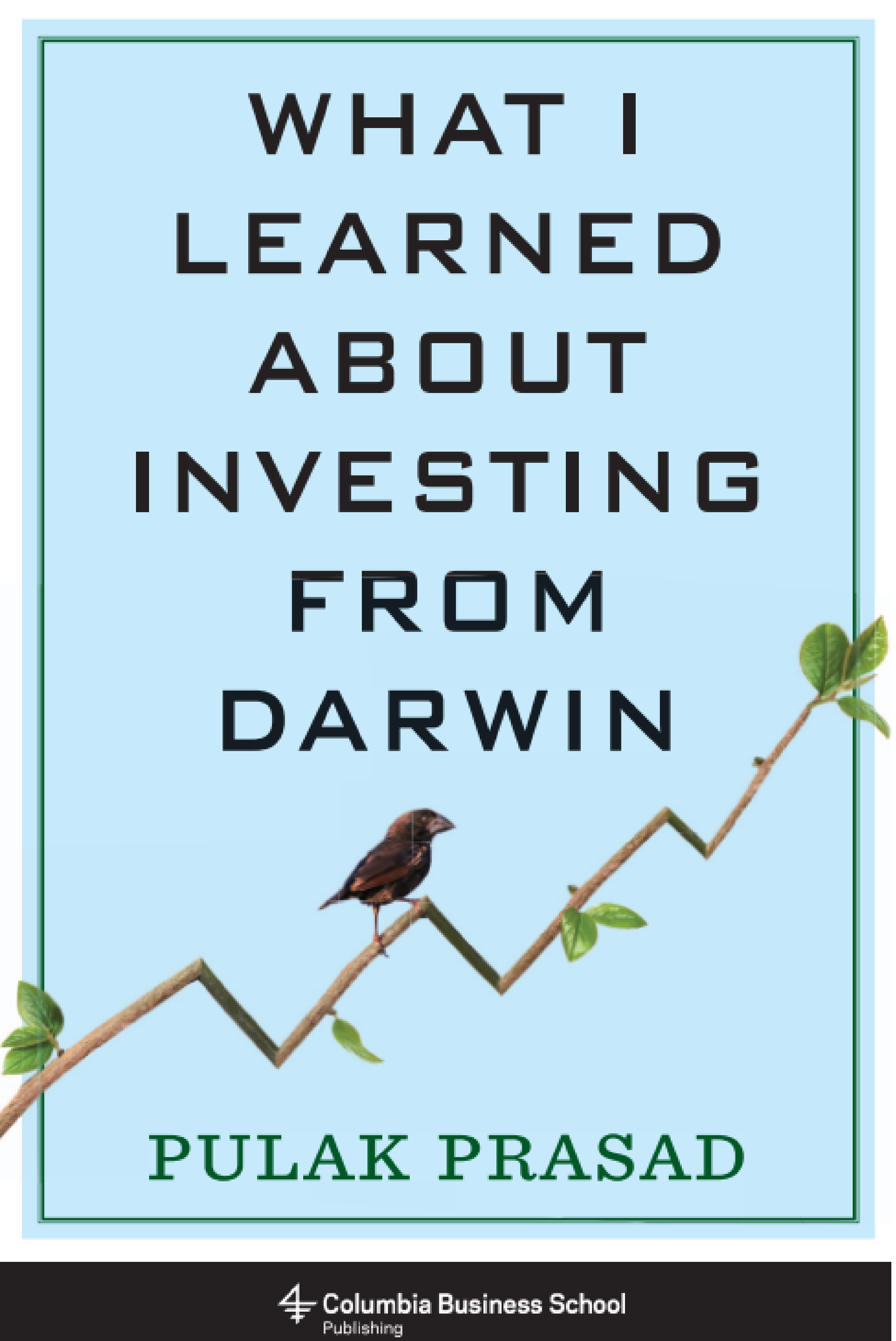

OLIVETTI


U2
THE
JOSHUA
TREE

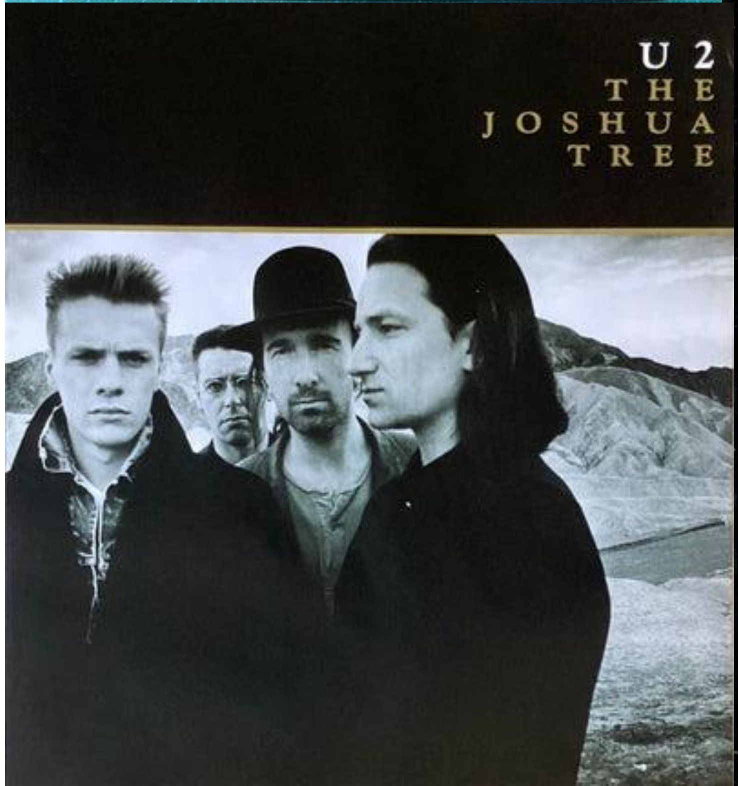

EVOLUTION AND COGNITION
The Origin and
Evolution of Cultures
Robert Boyd
Peter J. Richerson

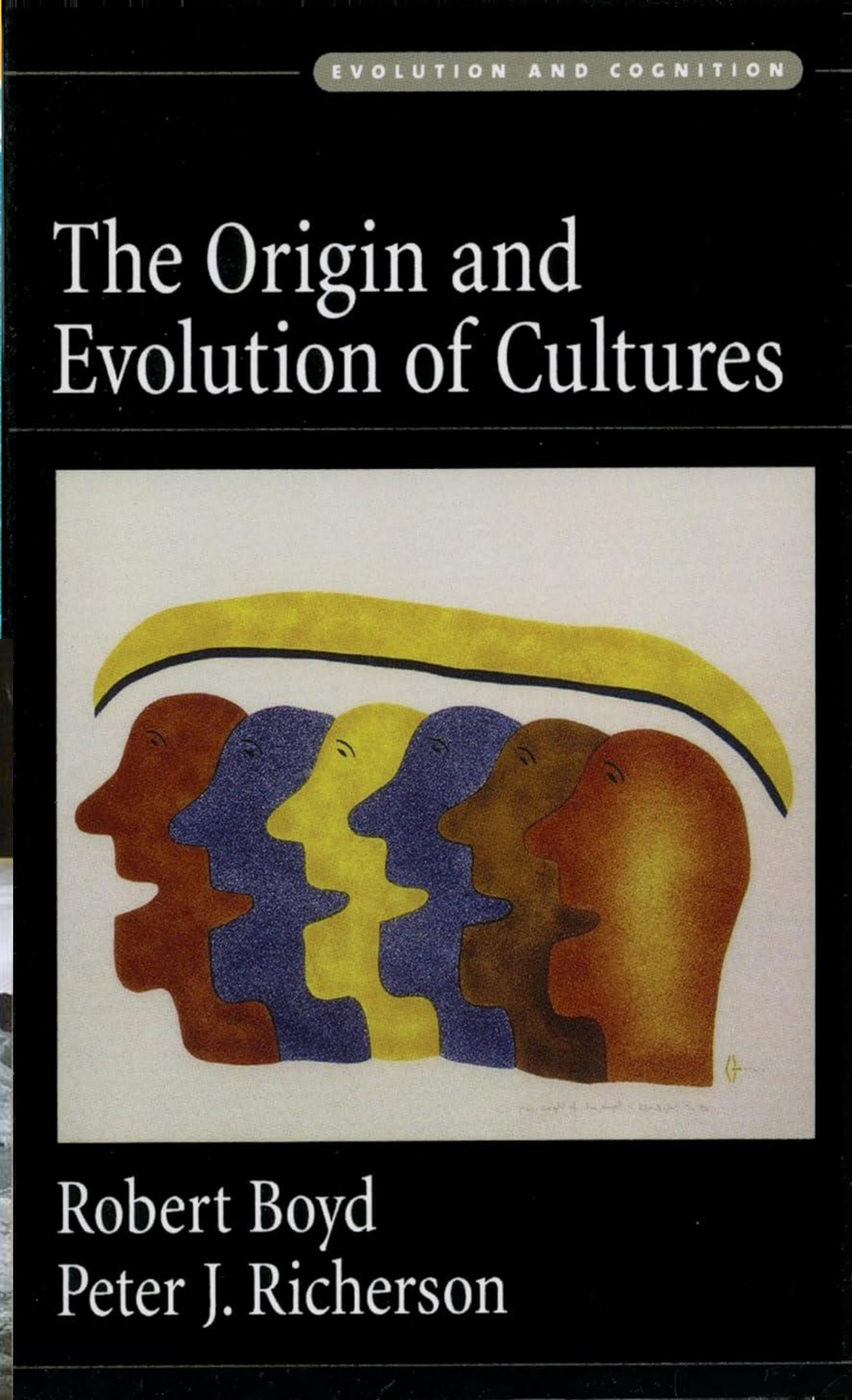
Evolutionary responses to environmental change

Fabrizio Mafessoni, Biologia Evoluzionistica 2025/2026, Università di Trieste



http://typewriterdatabase.com/my.10345.typewriter





Types of environmental change

Caused by:

- **External**
  - Climate change
  - Geological events
  - Ecological fluctuations
  - …
- **Evolutionary processes**:
  - **Frequency dependence** (social or ecological environment) and coevolutionary processes (e.g. Red Queen)
  - **Niche construction** (environmental feedbacks caused by evolution)

Types of environmental change

Temporal mode:

- **Gradual**
  - If very gradual, directional selection
  - The possibility to adapt depends on the pace of change
- **Abrupt**
  - Response is usually just extinction
- **Uncertain**
  - Bet-hedging
  - Plasticity and learning

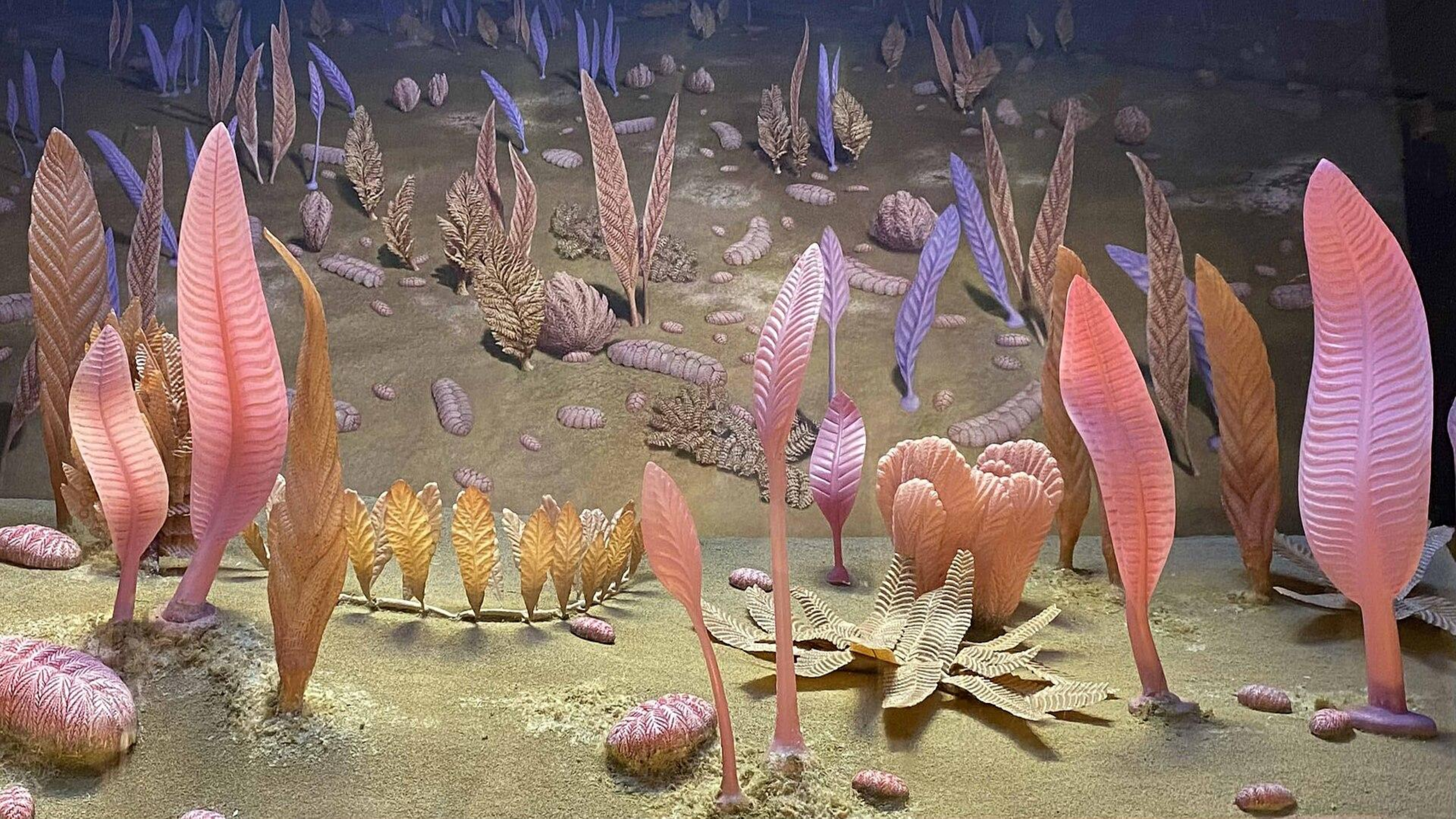
Types of environmental change

Temporal mode:

- **Gradual**
  - If very gradual, directional selection
  - The possibility to adapt depends on the pace of change
- **Abrupt**
  - Response is usually just extinction

Precambrian (**Ediacaran) biota (~635–541 Ma)**

- First large, complex multicellular organisms
- Mostly **soft-bodied**, no hard skeletons
- Often **enigmatic body plans** (not clearly related to modern animals) with quilted / fractal-like structures
- Low ecological complexity: likely lived on or within **microbial mats** with low mobility and simple feeding modes (limited evidence of predation)



Cambrian explosion (~541 Ma)

Rapid diversification of **animal body plans** with appearance of most major **bilaterian groups**
Key innovations:
hard parts (shells, exoskeletons)
predation and thus emergence of **active movement** and **food webs**
burrowing disrupts microbial mats
increased ecological interactions

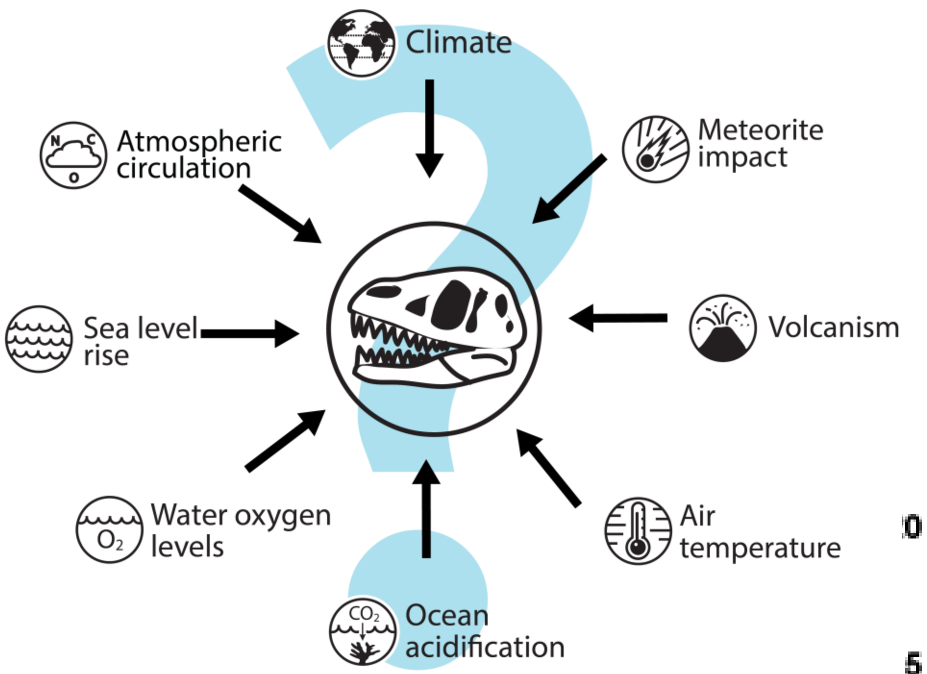
The five great mass extinctions

- **Ordovician–Silurian (~444 Ma)**
- **Late Devonian (~372–359 Ma)**
- **Permian–Triassic (~252 Ma)**

  "The Great Dying"
- **Triassic–Jurassic (~201 Ma)**
- **Cretaceous–Paleogene (~66 Ma)**

From National Geographic

What contributes to mass extinction?



The five great mass extinctions

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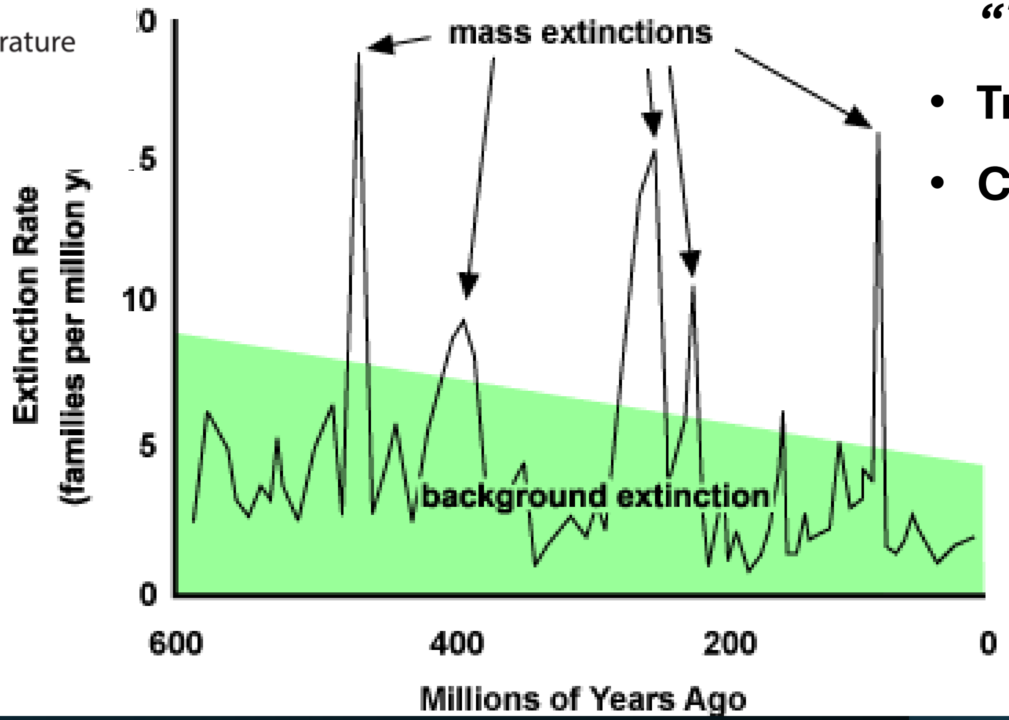


evolution.berkley.edu

Ordovician–Silurian (~444 Ma)

Likely causes

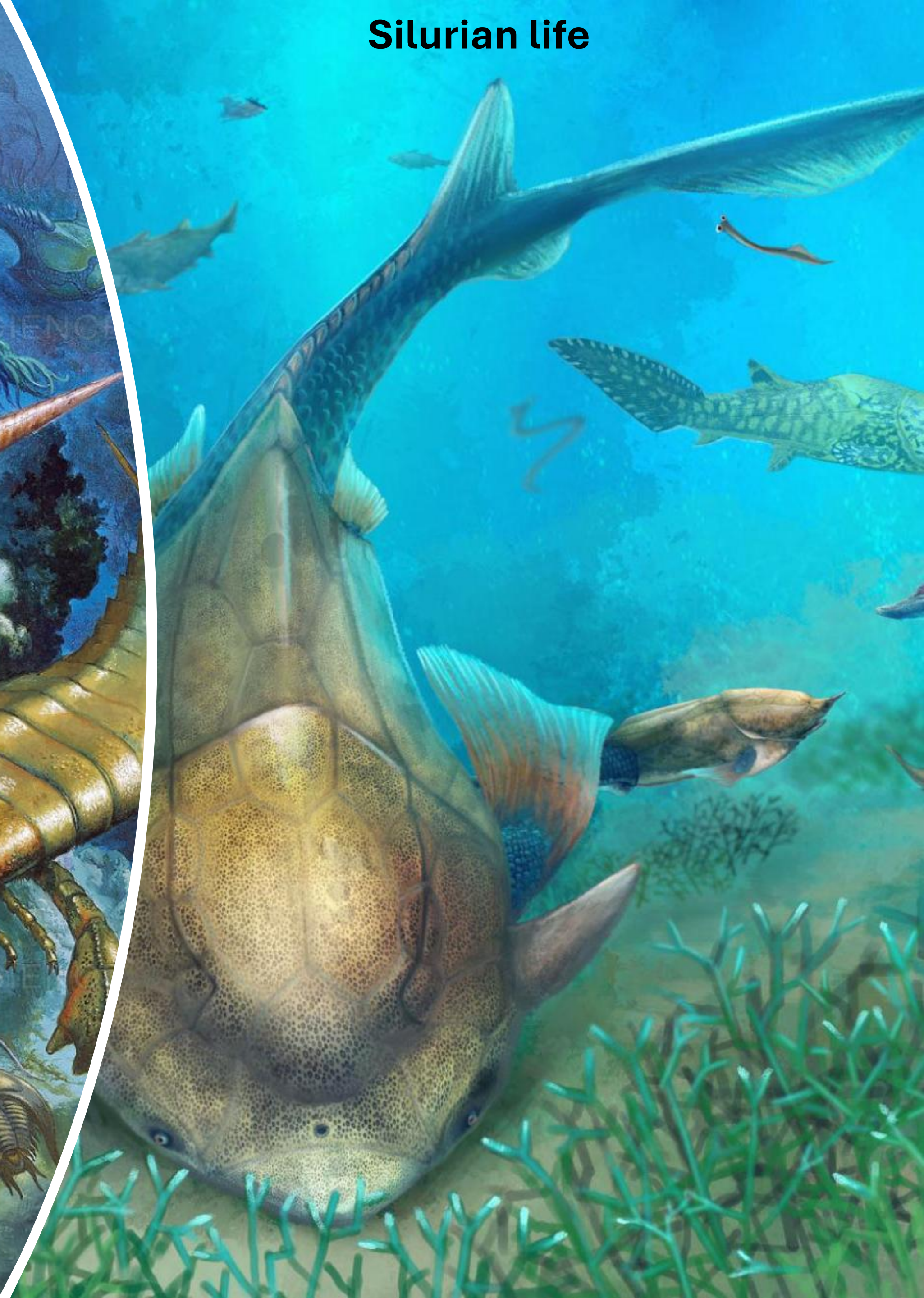
- Rapid **glaciation**
- Sea-level drop
- Cooling → habitat loss in shallow seas

Who was hit

- Marine invertebrates:
  - trilobites (many lineages)
  - brachiopods
  - bryozoans
- ~85% of marine species lost

Who benefited after

- surviving marine groups diversify
- early jawed vertebrates begin expanding



Late Devonian (~372–359 Ma)

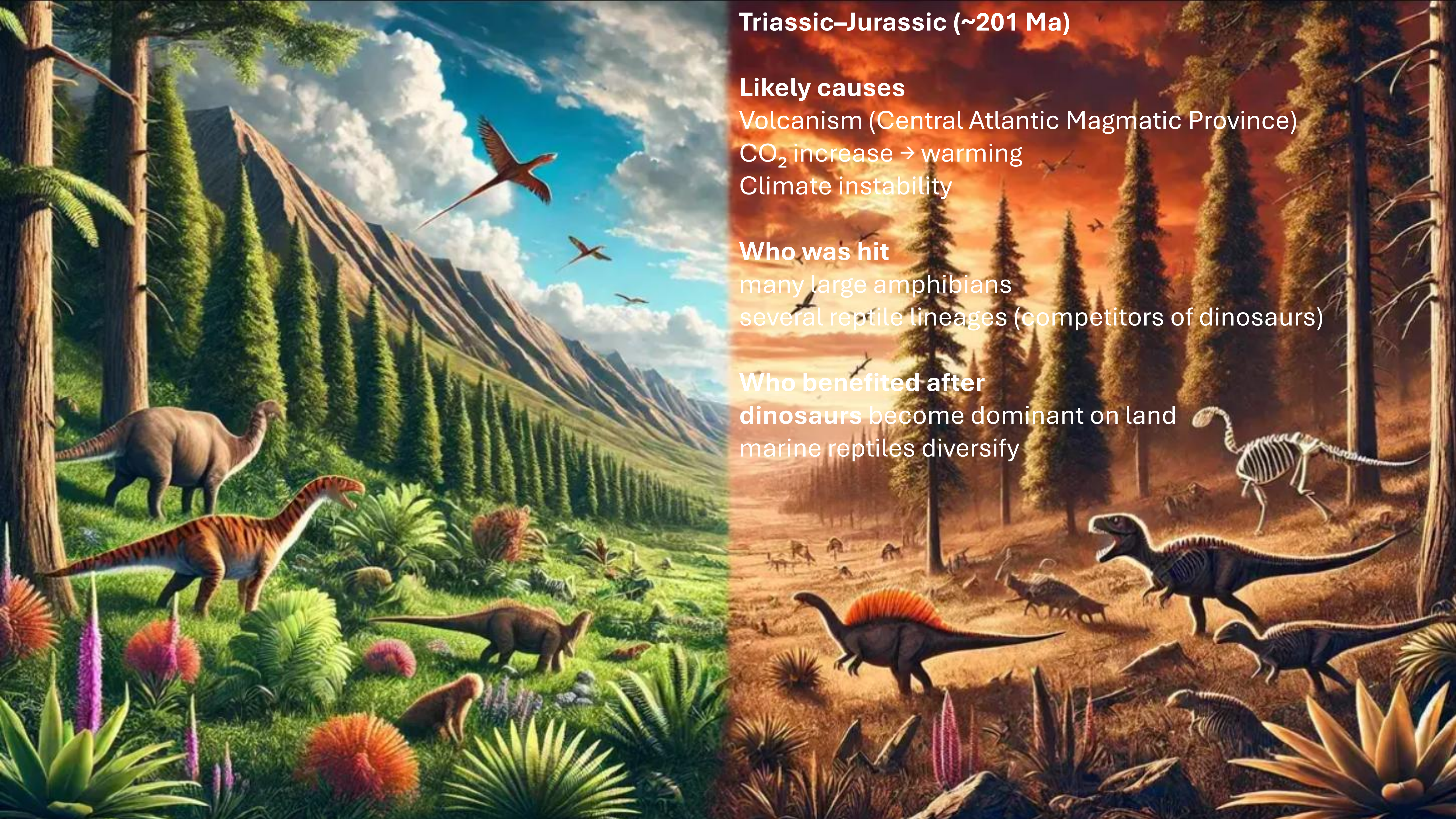
- **Likely causes:**
- Ocean **anoxia, p**ossibly partly driven by plants land plants and spread of forest, which led to mass flow of soil and nutrients into oceans
- Climate instability
- **Who was hit**
- Reef ecosystems collapse:
  - stromatoporoids
  - corals
- many armored fishes (**placoderms**)
- **Who benefited after**
- modern-style coral reefs later re-emerge
- ray-finned fishes diversify

Permian–Triassic (~252 Ma)
“The Great Dying”

Likely causes

- Massive volcanism (Siberian Traps)
- Extreme **global warming** (+5–10°C or more)
- Ocean anoxia and acidification

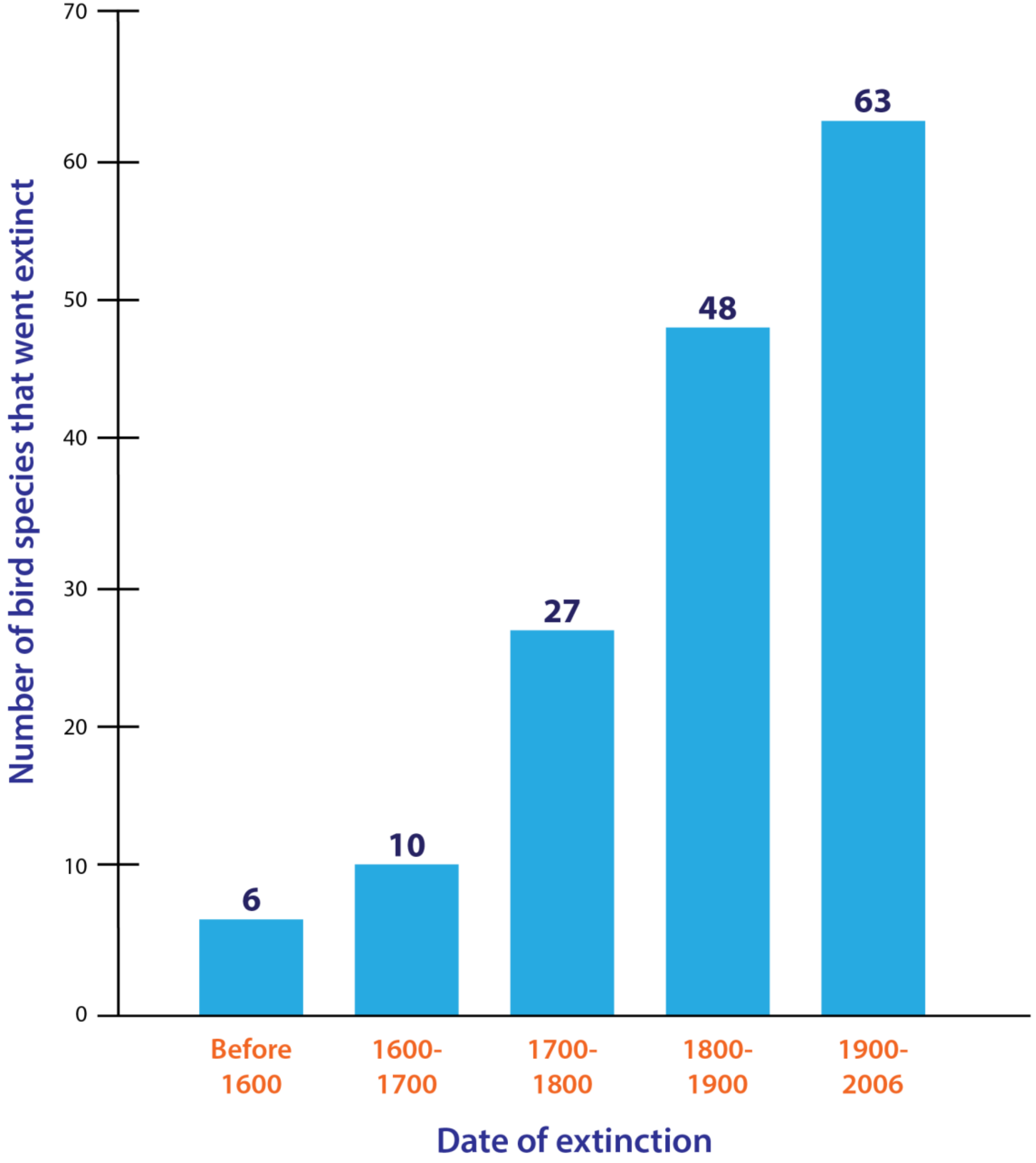
- **Who was hit**
  - ~90–95% of marine species (trilobites → **extinct**)
  - ~70% of terrestrial vertebrates lost
  - many insect and vertebrate groups collapse
- **Who benefited after**
  - early **archosaurs** (ancestors of dinosaurs)
  - modern insect groups expand
  - new marine faunas emerge
  - Ferns during collapse; early gymnosperms (gyngkos) later replaced by cycads


Triassic–Jurassic (~201 Ma)
Likely causes
Volcanism (Central Atlantic Magmatic Province)
CO_2 increase → warming
Climate instability
Who was hit
many large amphibians
several reptile lineages (competitors of dinosaurs)
Who benefited after
dinosaurs become dominant on land
marine reptiles diversify

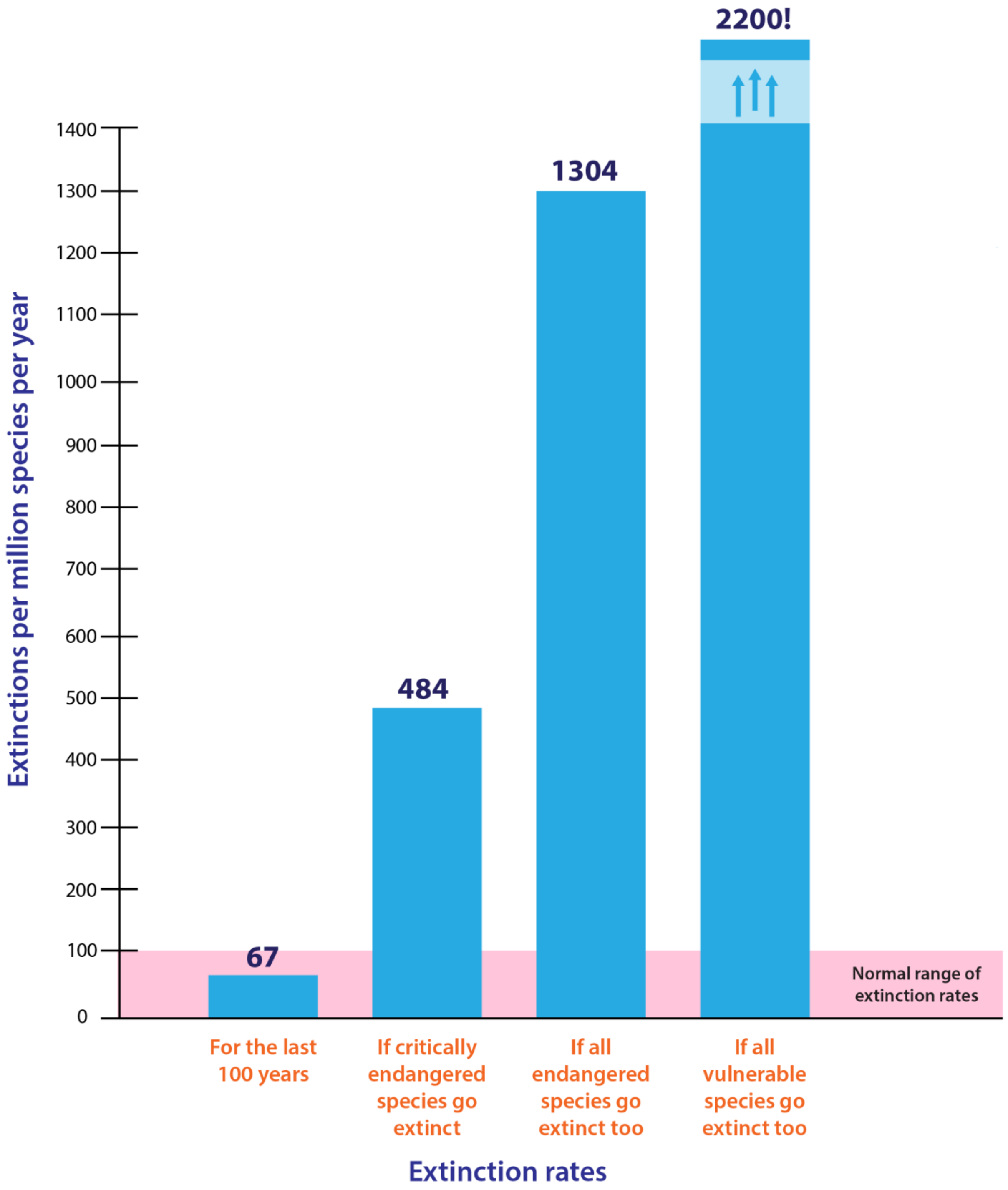
Cretaceous–Paleogene (~66 Ma)

- **Likely causes**
  - Asteroid impact (Chicxulub crater)
  - Possibly combined with volcanism (Deccan Traps)
  - Dust → darkness → collapse of photosynthesis
- **Who was hit**
  - non-avian **dinosaurs**
  - ammonites
  - many marine reptiles
- **Who benefited after**
  - **mammals** diversify
  - birds (avian dinosaurs) expand
  - flowering plant ecosystems restructure

Palaeopropithecus ingens
Extinct c. 1300-1400
Atelopus vogli
Extinct c. 1970s-1980s
Conuropsis carolinensis
Extinct c. 1910
Ara tricolor
Extinct c. 1885
Dusicyon australis
Extinct c. 1870s
Pinguinus impennus
Extinct c. 1852
Hydrodamalis gigas
Extinct c. 1768
Neomonachus tropicalis
Extinct c. 1960
Aepyornis maximus
Extinct c. 1000
Hoplodactylus delcourti
Extinct c. 1870s-1900s (but unclear date)
Ectopistes migratorius
Extinct c. 1905
Anolis roosevelti
Extinct c. 1980



Number of bird species that went extinct
0
10
20
30
40
50
60
70
6
10
27
48
63
Before 1600
1600-1700
1700-1800
1800-1900
1900-2006
Date of extinction



Extinctions per million species per year
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
67
484
1304
2200!
Normal range of extinction rates
For the last 100 years
If critically endangered species go extinct
If all endangered species go extinct too
If all vulnerable species go extinct too
Extinction rates

MASS EXTINCTIONS

A mass extinction is a sharp spike in the rate of extinction of species caused by a catastrophic event or rapid environmental change. Scientists have been able to identify five mass extinctions in Earth's history, each of which led to a loss of more than 75 percent of animal species.

NATIONAL GEOGRAPHIC

1. ORDOVICIAN-SILURIAN EXTINCTION 440 MILLION YEARS AGO (MA)

86% LOSS

Scientists theorize that there were two main phases to this extinction: a glaciation event and a heating event. Abundant plant life removed carbon dioxide (CO_2) from the air, causing global cooling and glacier formation. This led to a drop in sea levels, reducing habitat. Later came global warming and sea level rising again. Creatures that had adapted to the cooler climate were unable to survive the increased temperature. Since most fauna was marine at the time, 86% of life was lost.

2. LATE DEVONIAN EXTINCTION—365 MA

75% LOSS

About 75% of life died off during this period. One theory suggests that land plants developed deep roots, releasing an abundance of nutrients into the oceans that fed algae. Because of this, algae blooms consumed vast amounts of oxygen (O_2) in the oceans, suffocating many species. Another theory suggests that another global cooling took place, resulting in glaciation and a fall in sea level, leading to habitat loss.

3. PERMIAN-TRIASSIC EXTINCTION—252 MA

96% LOSS

The Permian-Triassic was the deadliest extinction in history: 96% of all life perished. Scientist believe that volcanic activity in Siberia put massive amounts of carbon dioxide, a greenhouse gas, into the atmosphere. Bacteria that thrive on CO_2 began producing methane, another greenhouse gas. Large quantities of both gases warmed the planet and combined with Earth's water, making the ocean and rain acidic, creating a highly toxic environment for life.

4. TRIASSIC-JURASSIC EXTINCTION—201.3 MA

80% LOSS

Some scientists theorize that volcanic eruptions spewed tons of CO_2 into the atmosphere, which trapped heat and acidified the oceans, causing this mass extinction. Other scientists contend that an asteroid or comet impact triggered the extinction. About 80% of life was lost in this extinction, including most of the mammals, making way for the dinosaur's ancestors.

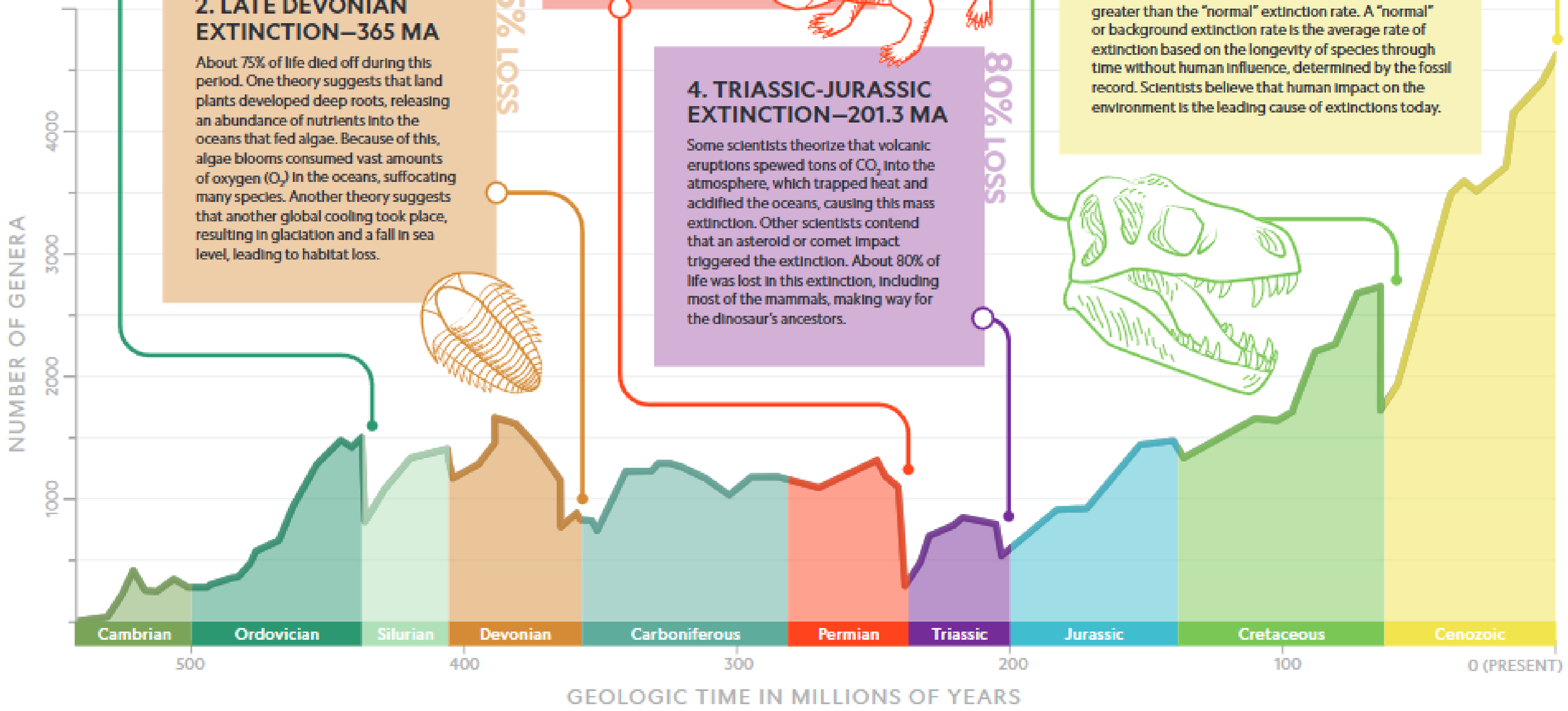
5. CRETACEOUS-PALEOGENE EXTINCTION—66 MA

60-76% LOSS

The Cretaceous-Paleogene extinction wiped out the dinosaurs, along with 60-76% of all life on Earth. A widely accepted theory is that an asteroid landed in the Yucatán Peninsula in Mexico and killed the dinosaurs. The impact would have ejected enormous amounts of debris into the atmosphere, causing global temperatures to drop. The impact may have also caused local fires, earthquakes, tsunamis, and acid rain.

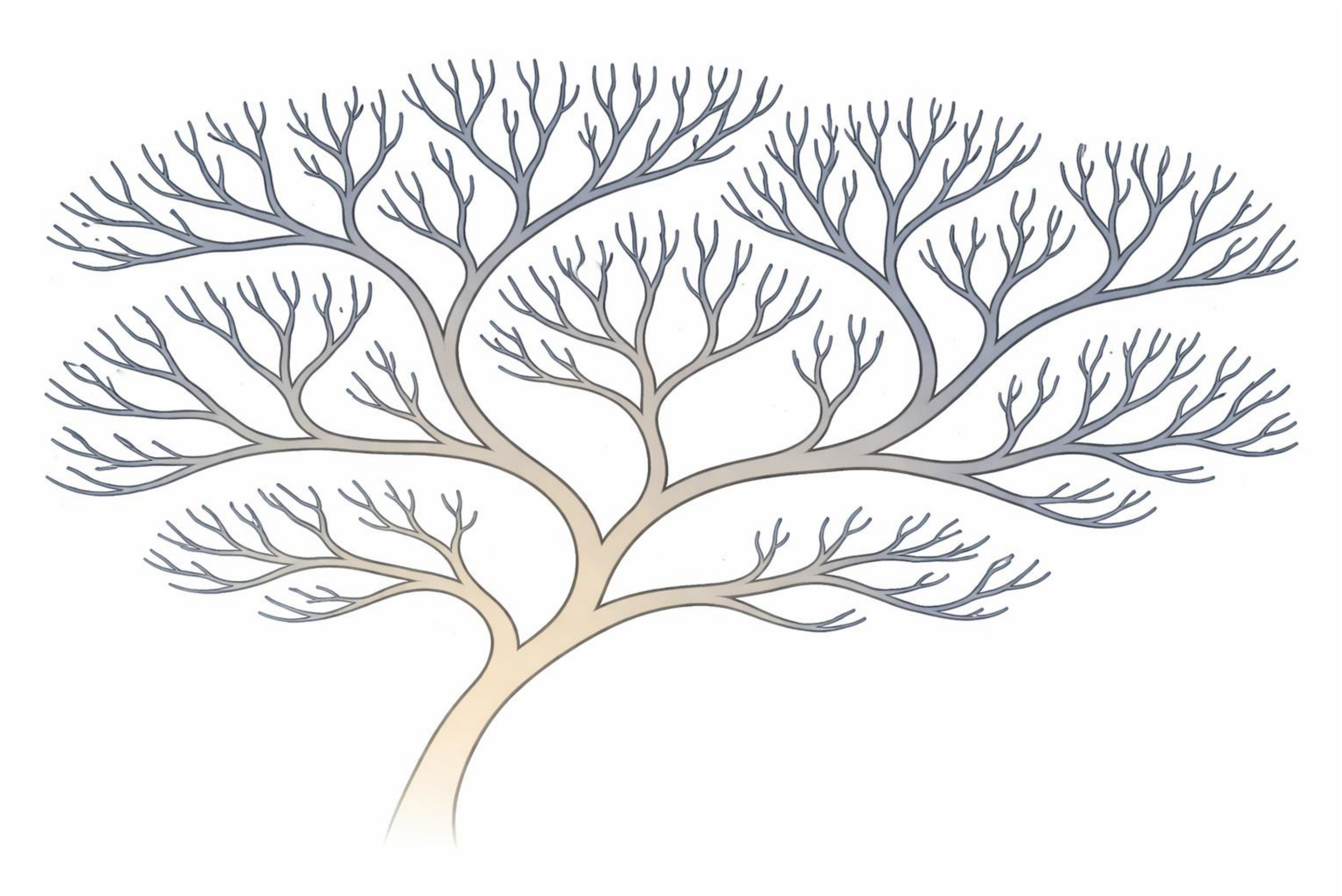
6. HOLOCENE EXTINCTION 11,700 YEARS AGO TO PRESENT

The next mass extinction may already be happening. The current extinction rate is at least a thousand times greater than the "normal" extinction rate. A "normal" or background extinction rate is the average rate of extinction based on the longevity of species through time without human influence, determined by the fossil record. Scientists believe that human impact on the environment is the leading cause of extinctions today.

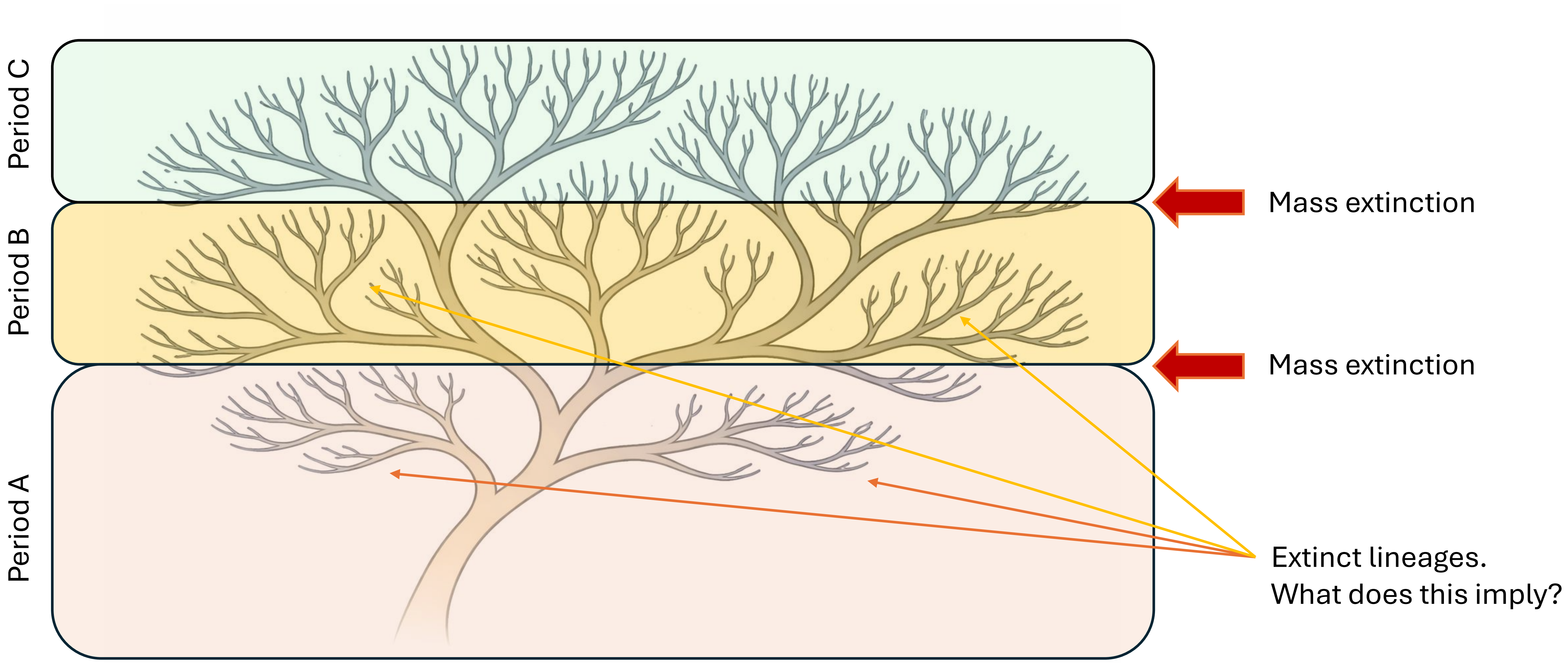


«If we replay the tape of evolution, will we get the same outcome?»

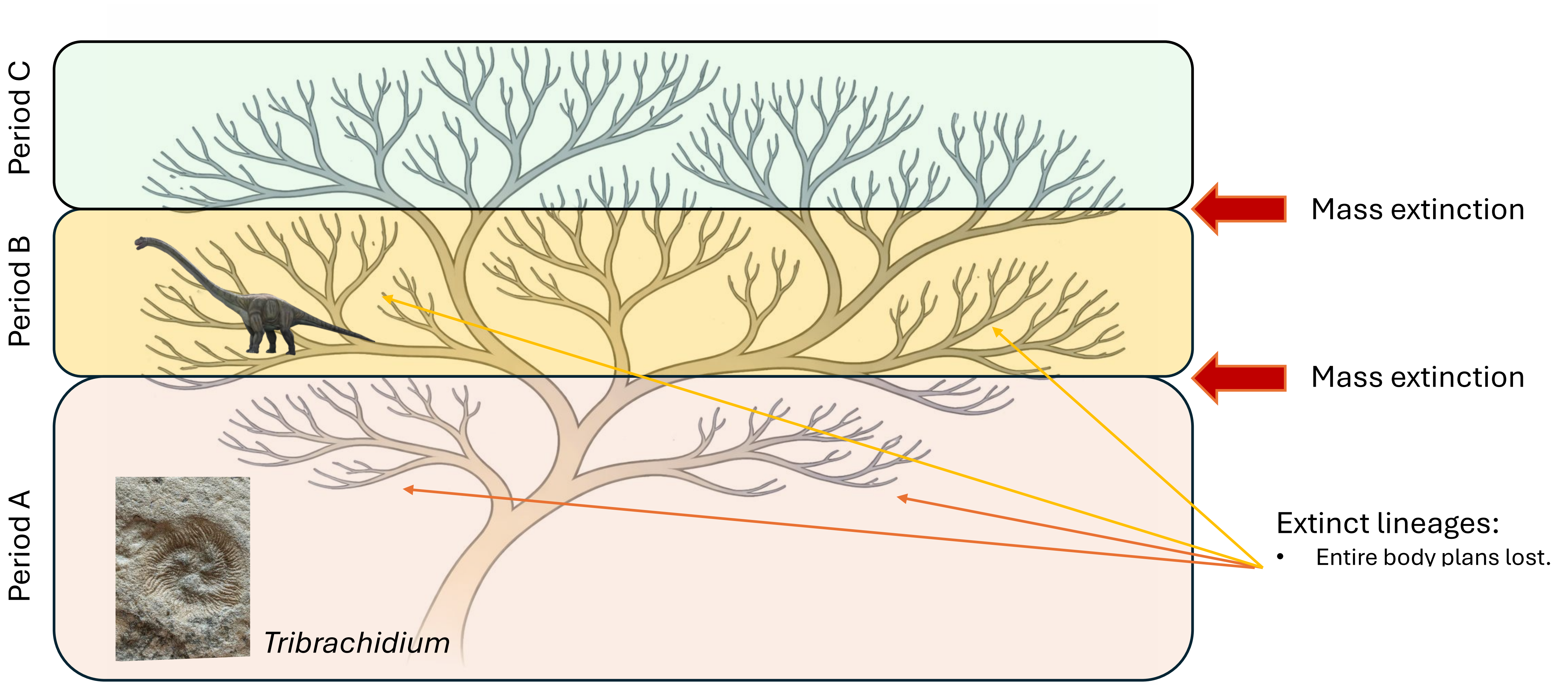
Abrupt events and mass extinction act as stochastic filters on surviving lineages



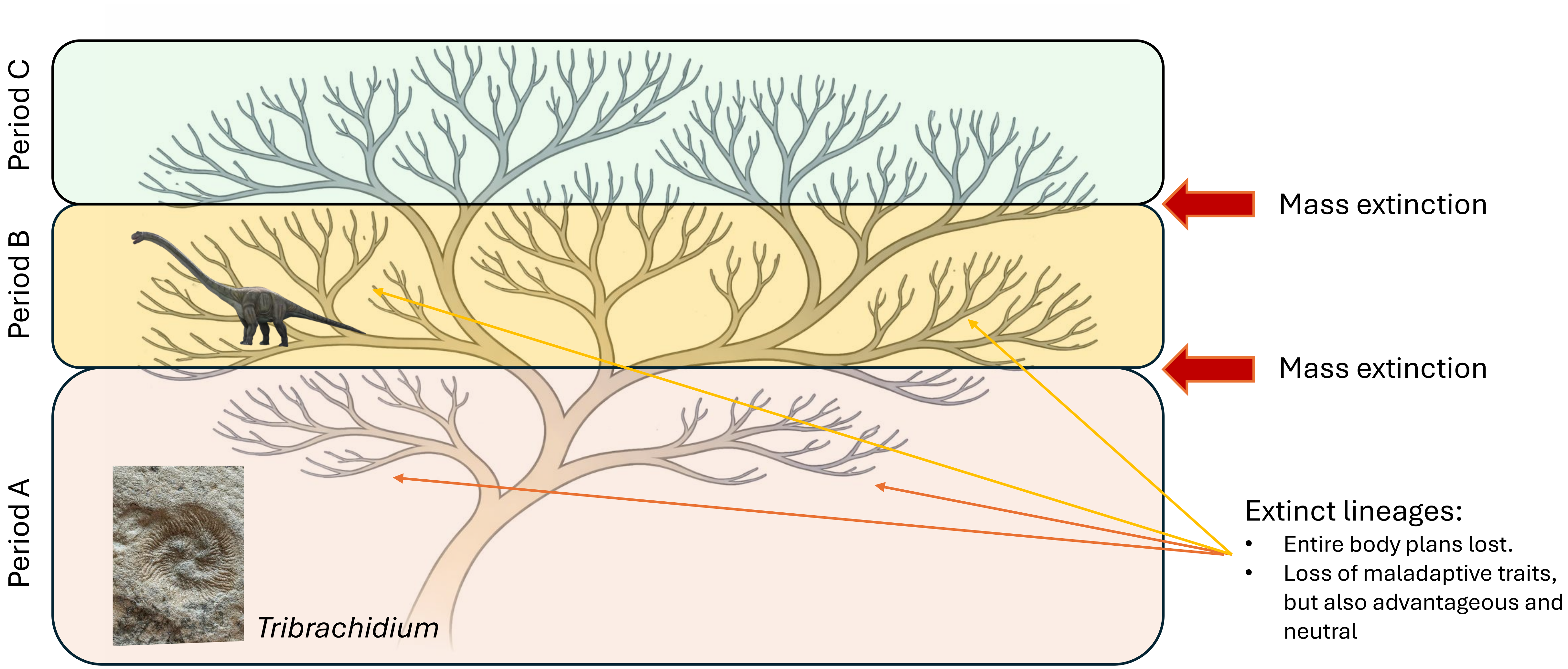
Abrupt events and mass extinction act as stochastic filters on surviving lineages



Abrupt events and mass extinction act as stochastic filters on surviving lineages

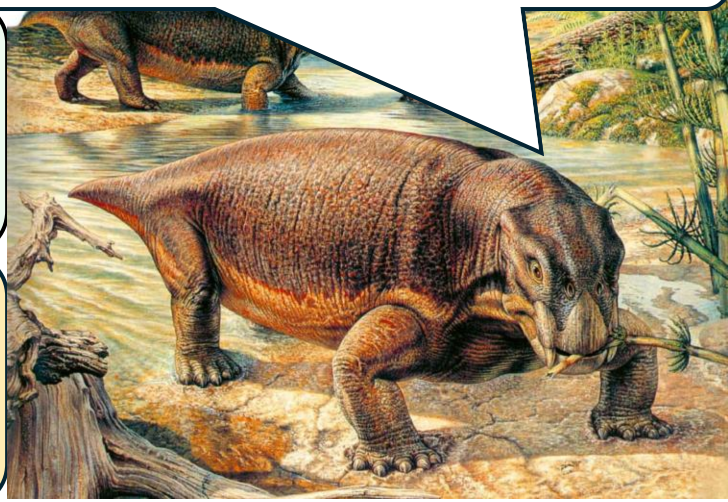


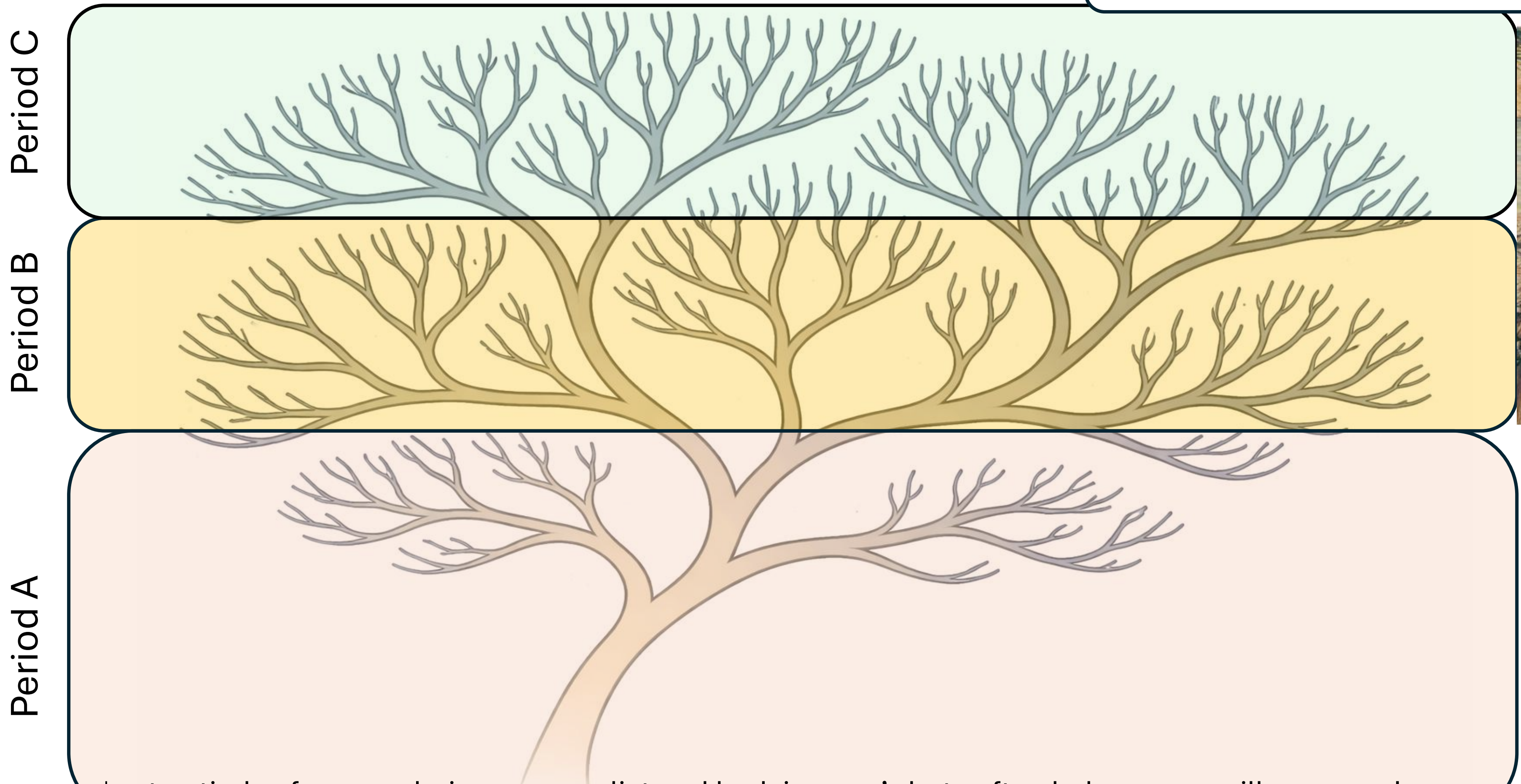
Abrupt events and mass extinction act as stochastic filters on surviving lineages



Abrupt events and mass extinction act as stochastic filters on surviving lineages

I am the Lystrosaurus, and while 95% of the species disappeared, I dominated after «the Great Dying» for millions of years. Maybe because I was burrowing and generalist diet. But was I so much «more evolved» than everybody else?

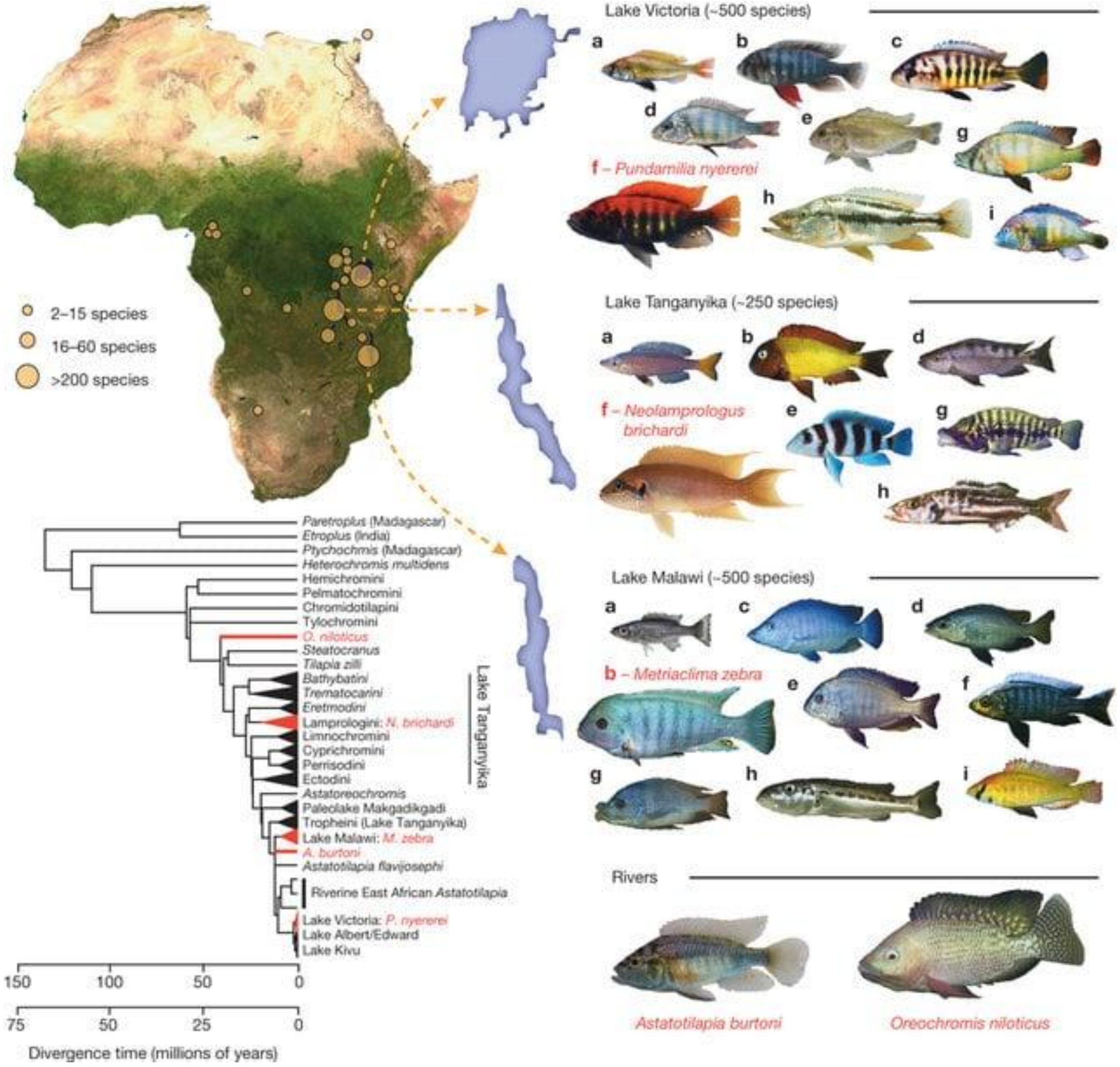


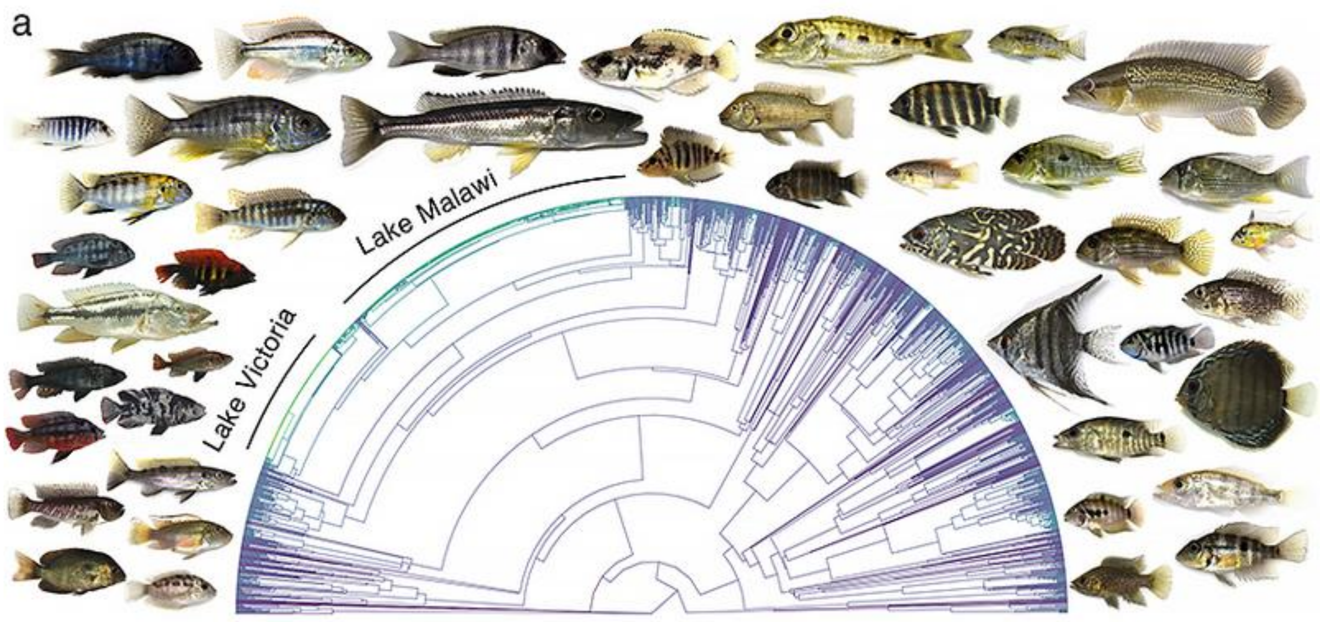


*not entirely of course, being a generalist and hedging one’s bets often helps as we will see soon!

The reasons why some dominant lineages disappear and some become dominant can be «quite*» random

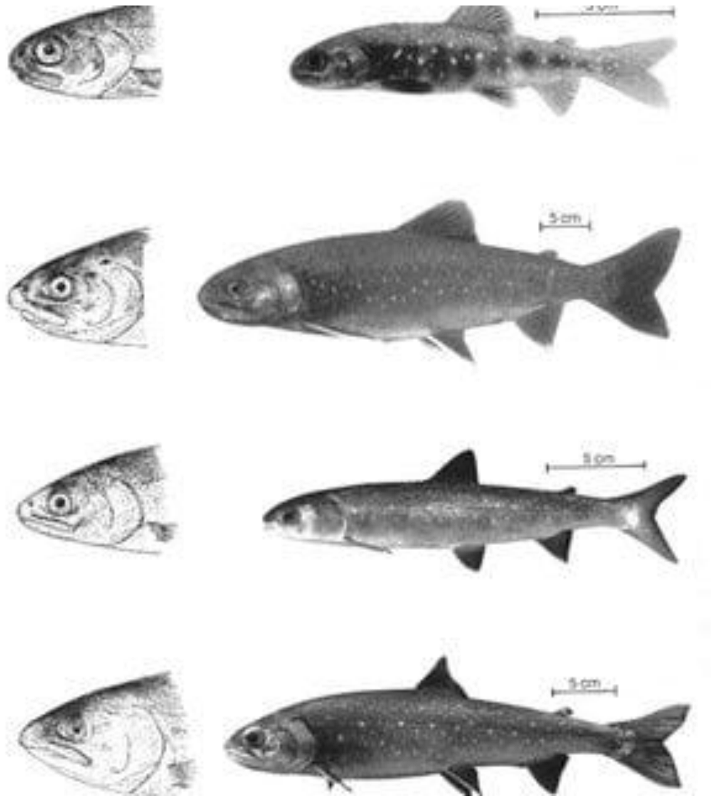
Adaptive radiations are also strongly determined by contingency



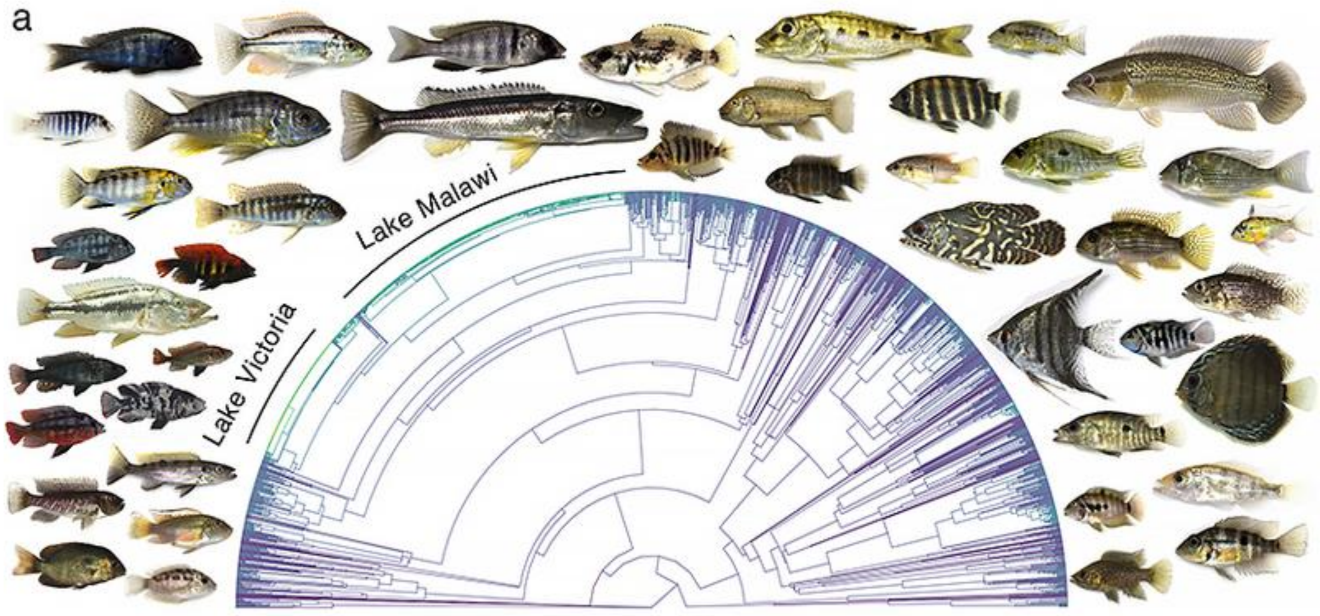


Cichlid radiations in African lakes

- Repeated and extreme (hundreds of species).
- Likely favoured by modular jaw structure (which allow flexible trophic specialization) and strong sexual selection (which favors diversification) → not entirely a chance but..

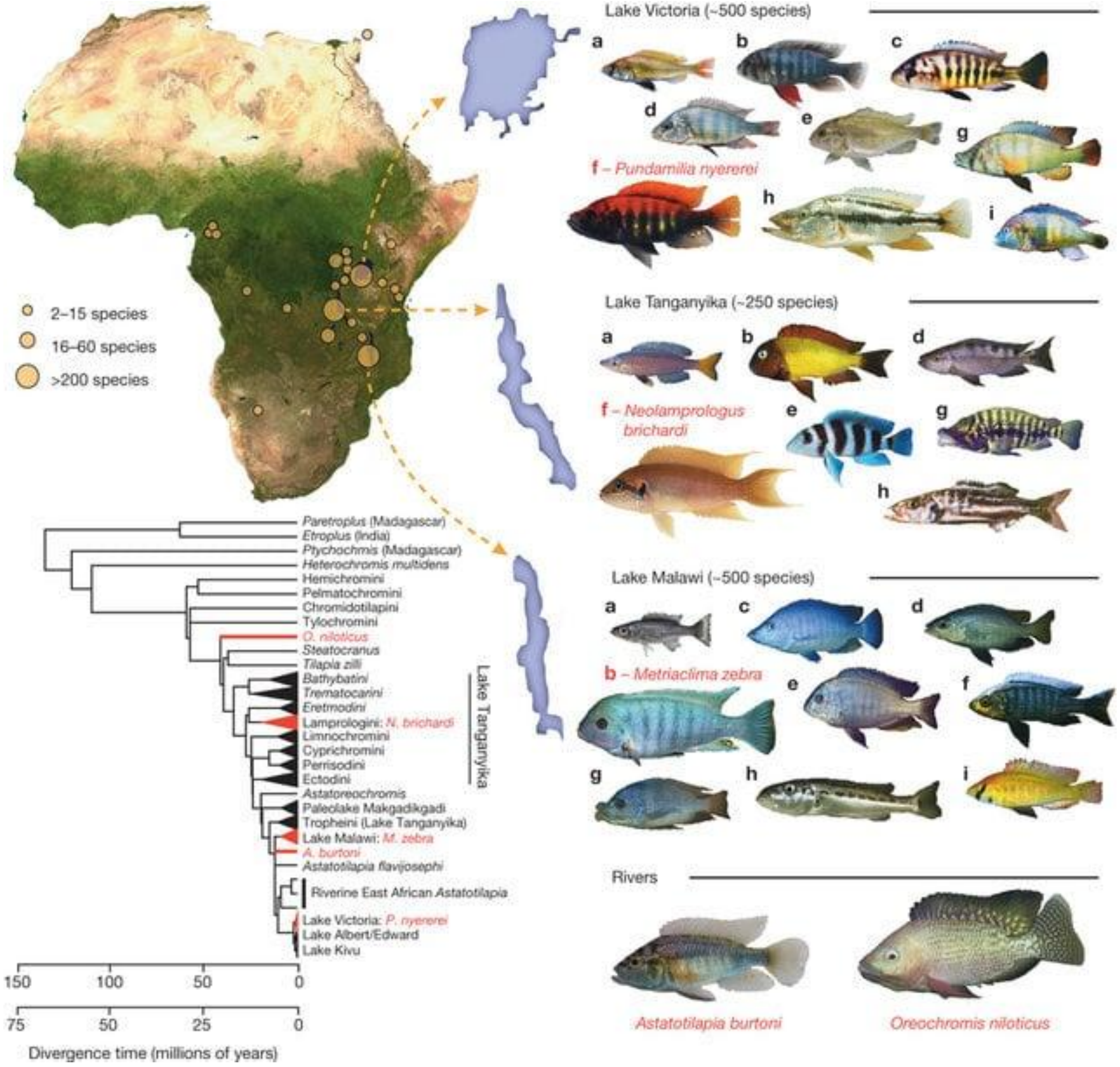


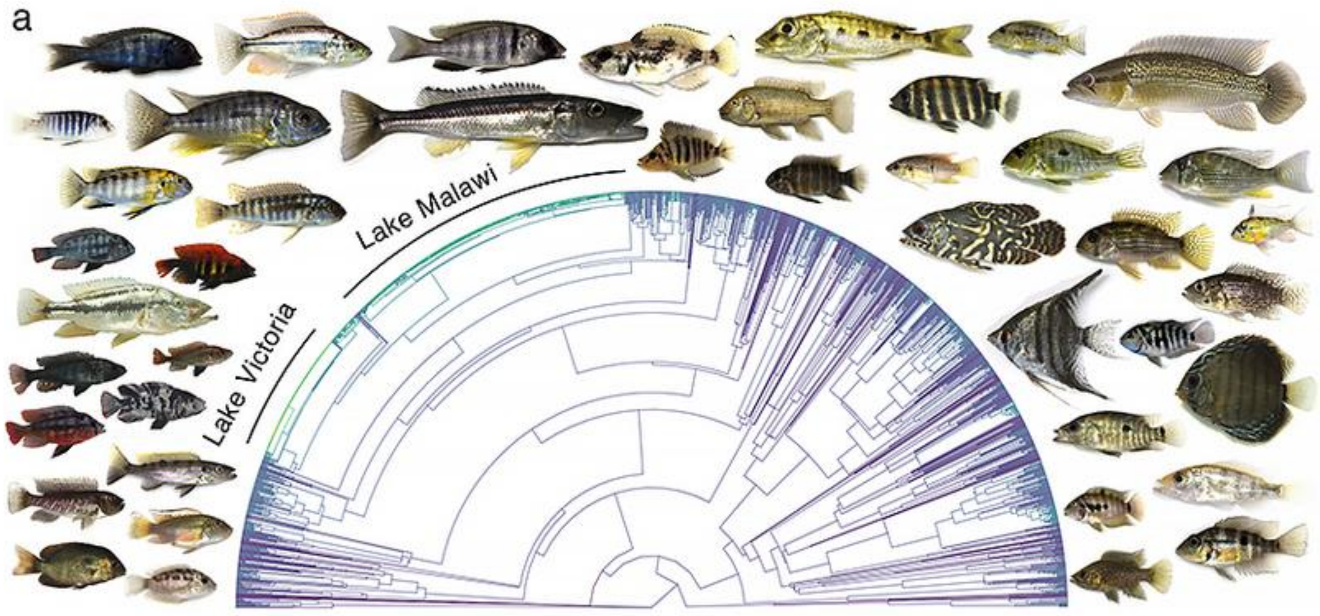
Different forms of arctic charr (*Salvelinus alpinus*) from Iceland (Michaud et al.,2006)



Cichlid radiations in African lakes

- Repeated and extreme (hundreds of species).
- Likely favoured by modular jaw structure (which allow flexible trophic specialization) and strong sexual selection (which favors diversification) → not entirely a chance but..
- ..In other lakes other fish dominate (and radiate, albeit less): pupfish (cyprinodon) in desert lakes, arctic charr in northen lakes (e.g. Iceland, Norway)



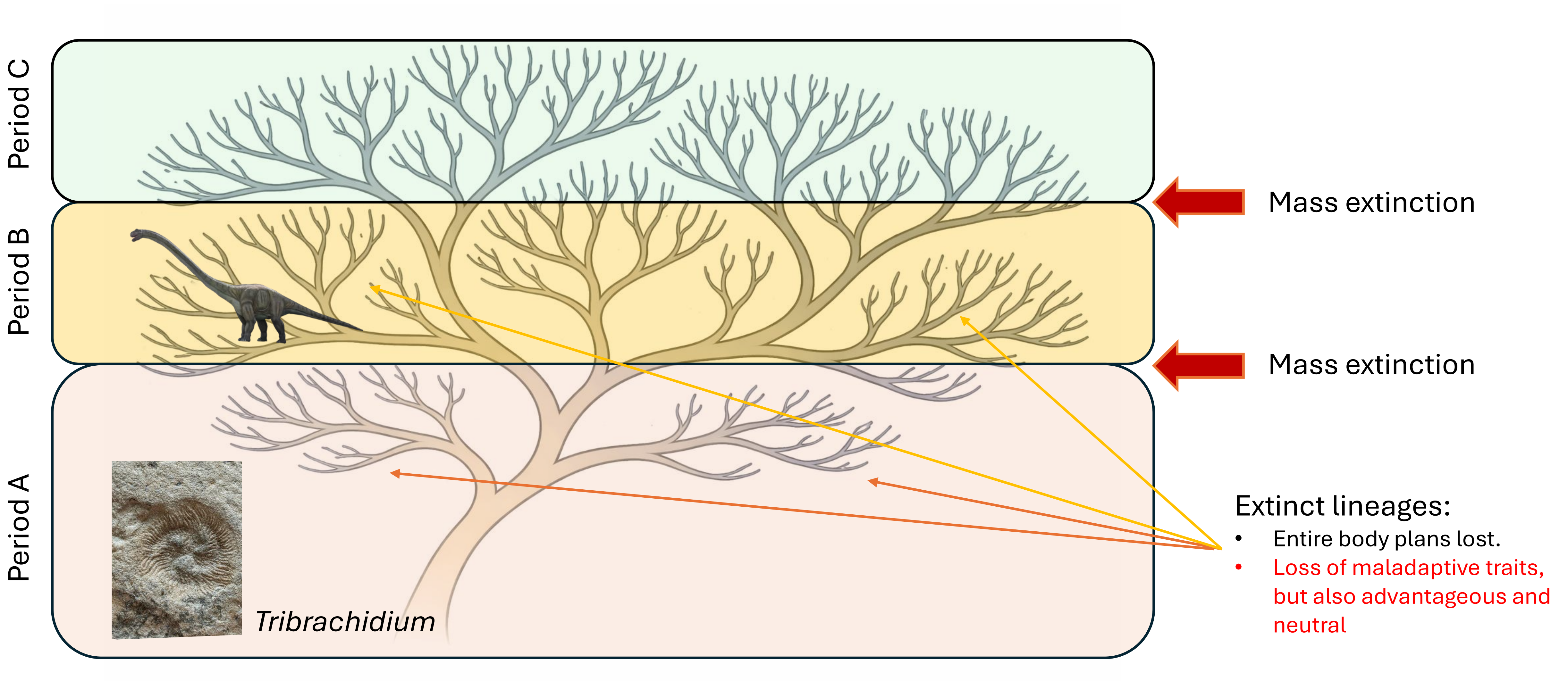


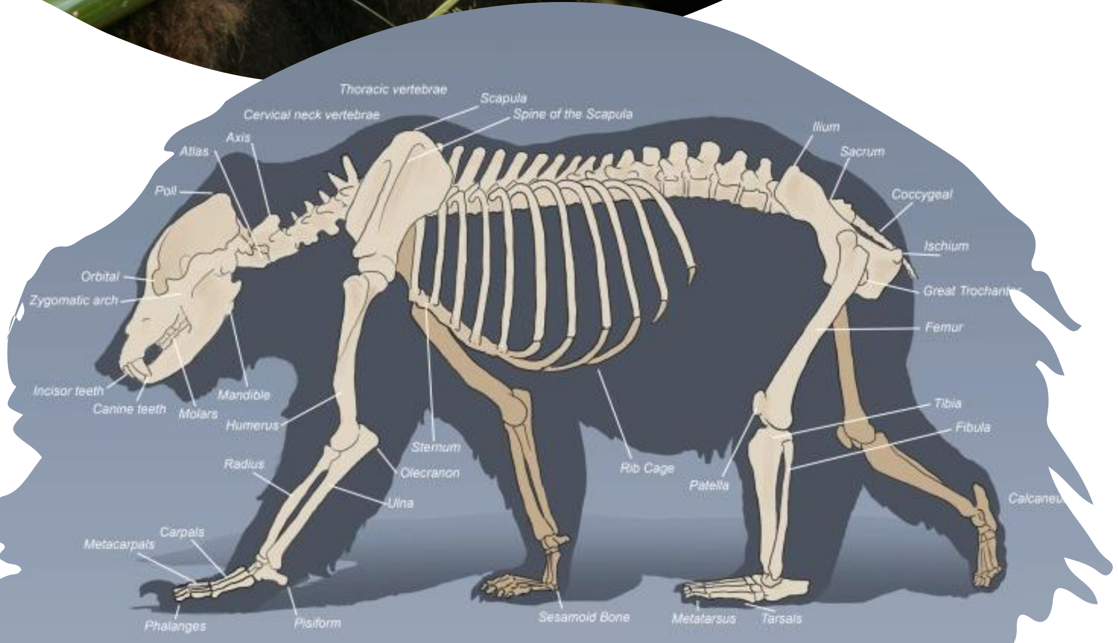
Cichlid radiations in African lakes

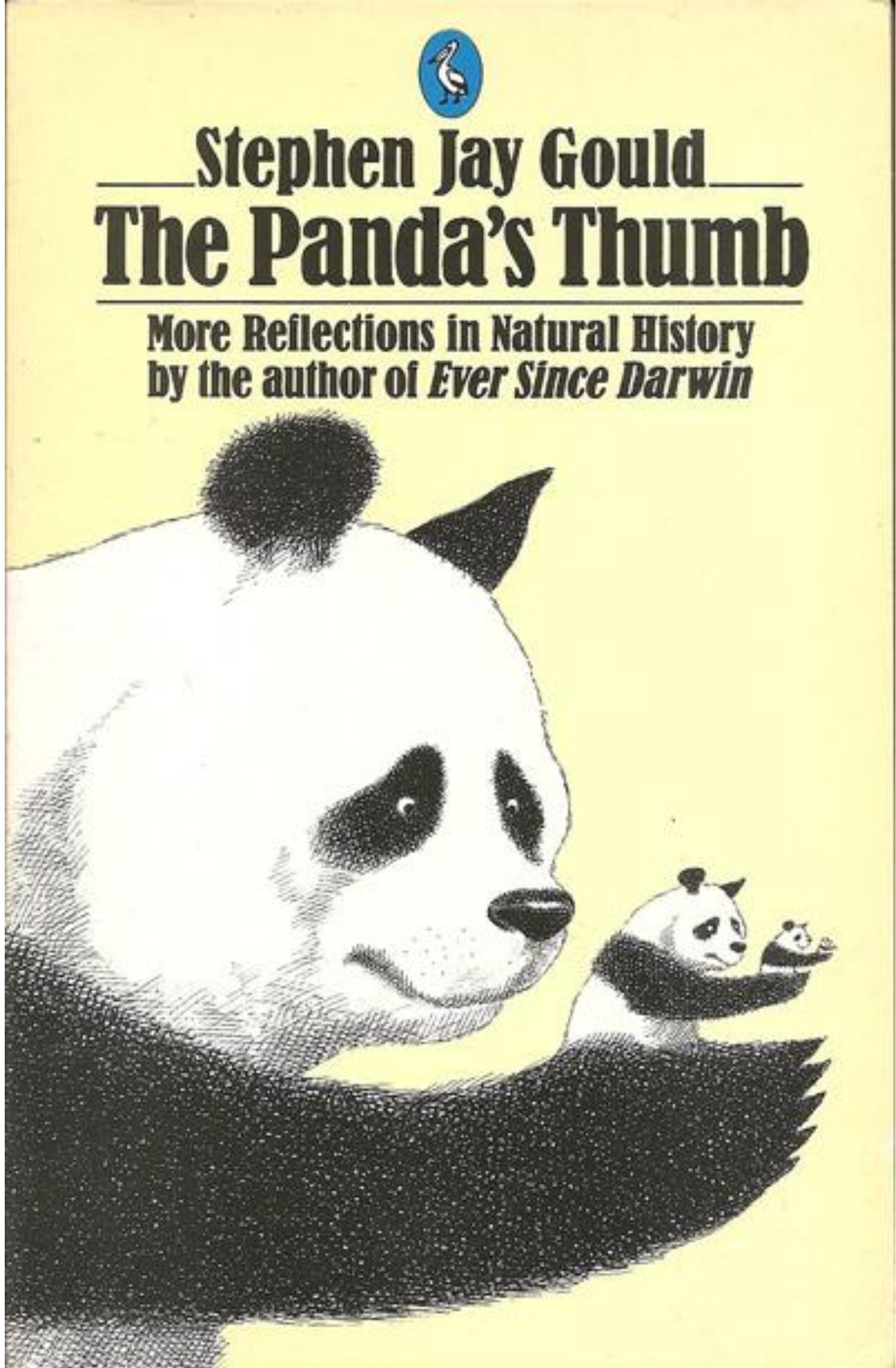
Winners in radiations and colonizations, like for mass extinctions, are lucky (strong stochasticity, who arrives first) – but not only.

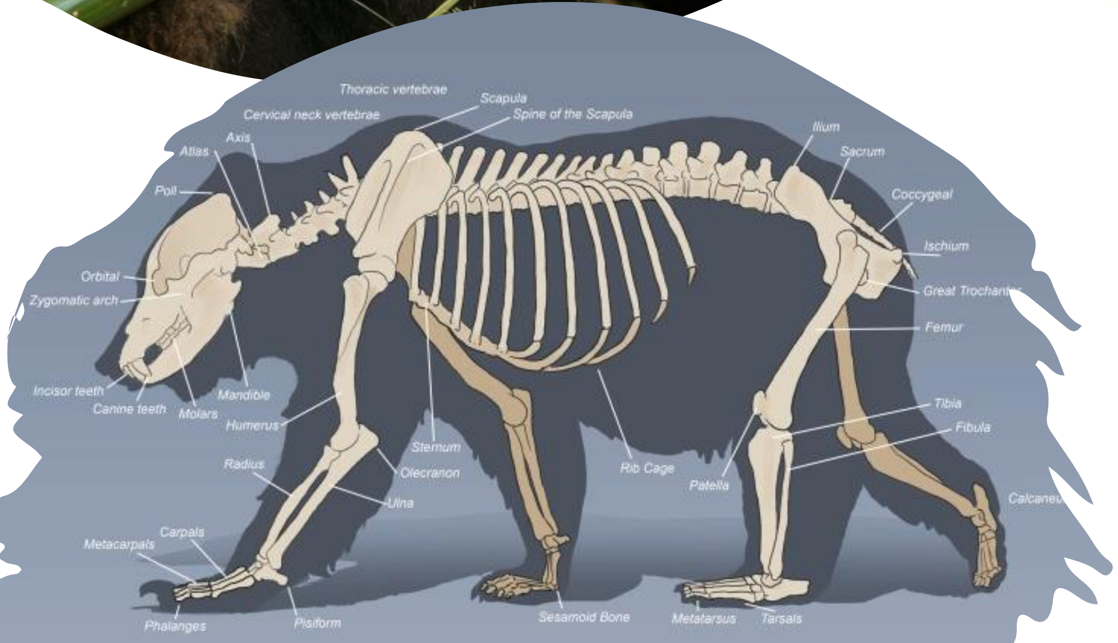
They are «biased winners».

Abrupt events and mass extinction act as stochastic filters on surviving lineages




Thoracic vertebrae
Scapula
Cervical neck vertebrae
Spine of the Scapula
Axis
Atlas
Poll
Ilium
Sacrum
Coccygeal
Ischium
Orbital
Zygomatic arch
Femur
Incisor teeth
Canine teeth
Molars
Mandible
Humerus
Tibia
Fibula
Sternum
Radius
Olecranon
Ulna
Rib Cage
Patella
Carpals
Metacarpals
Phalanges
Pisiform
Sesamoid Bone
Metatarsus
Tarsals


Stephen Jay Gould
The Panda's Thumb
More Reflections in Natural History
by the author of Ever Since Darwin


Thoracic vertebrae
Scapula
Cervical neck vertebrae
Spine of the Scapula
Axis
Atlas
Poll
Ilium
Sacrum
Coccygeal
Ischium
Orbital
Zygomatic arch
Great Trochant
Femur
Incisor teeth
Canine teeth
Molars
Mandible
Humerus
Tibia
Fibula
Sternum
Olecranon
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Carpals
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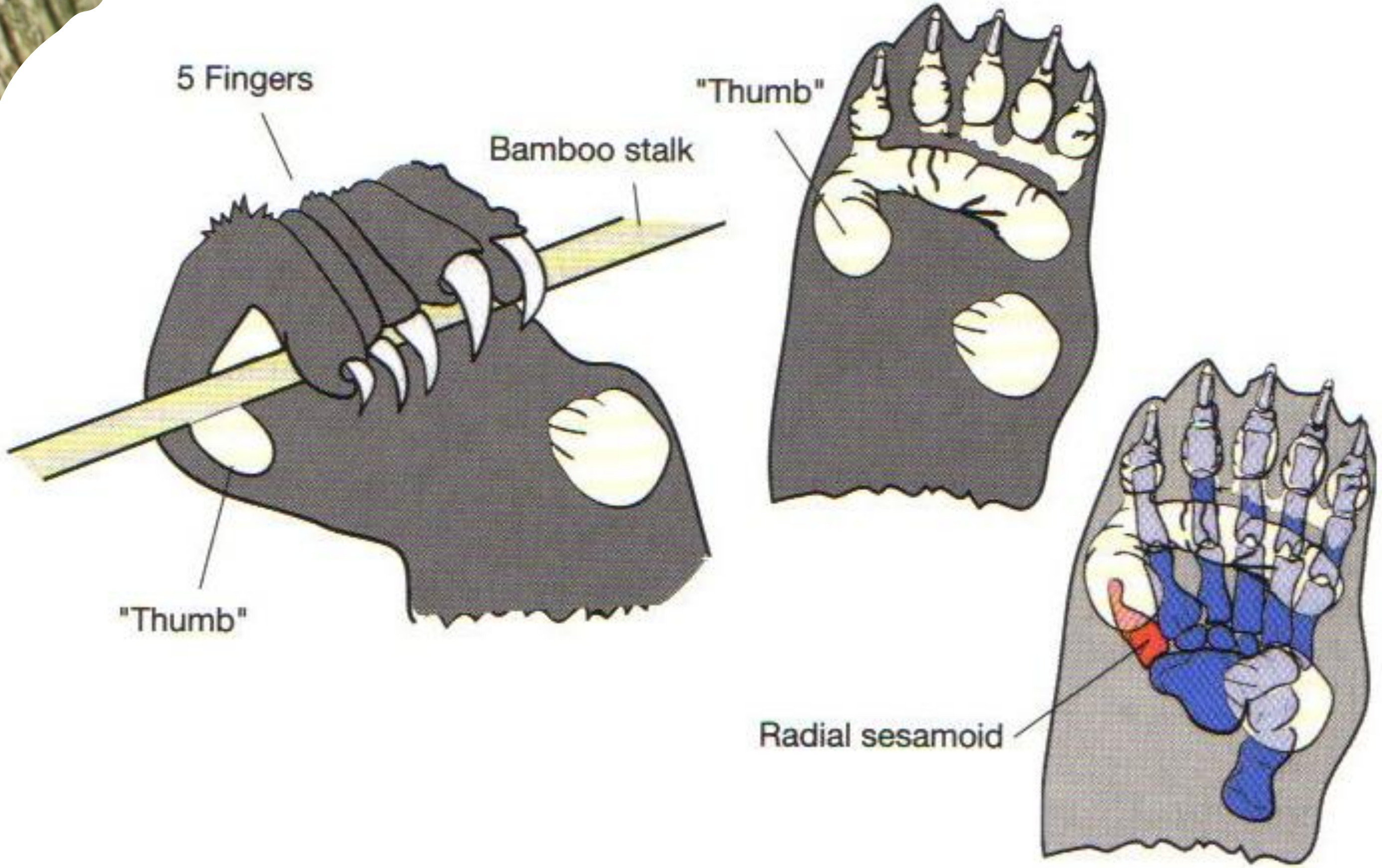
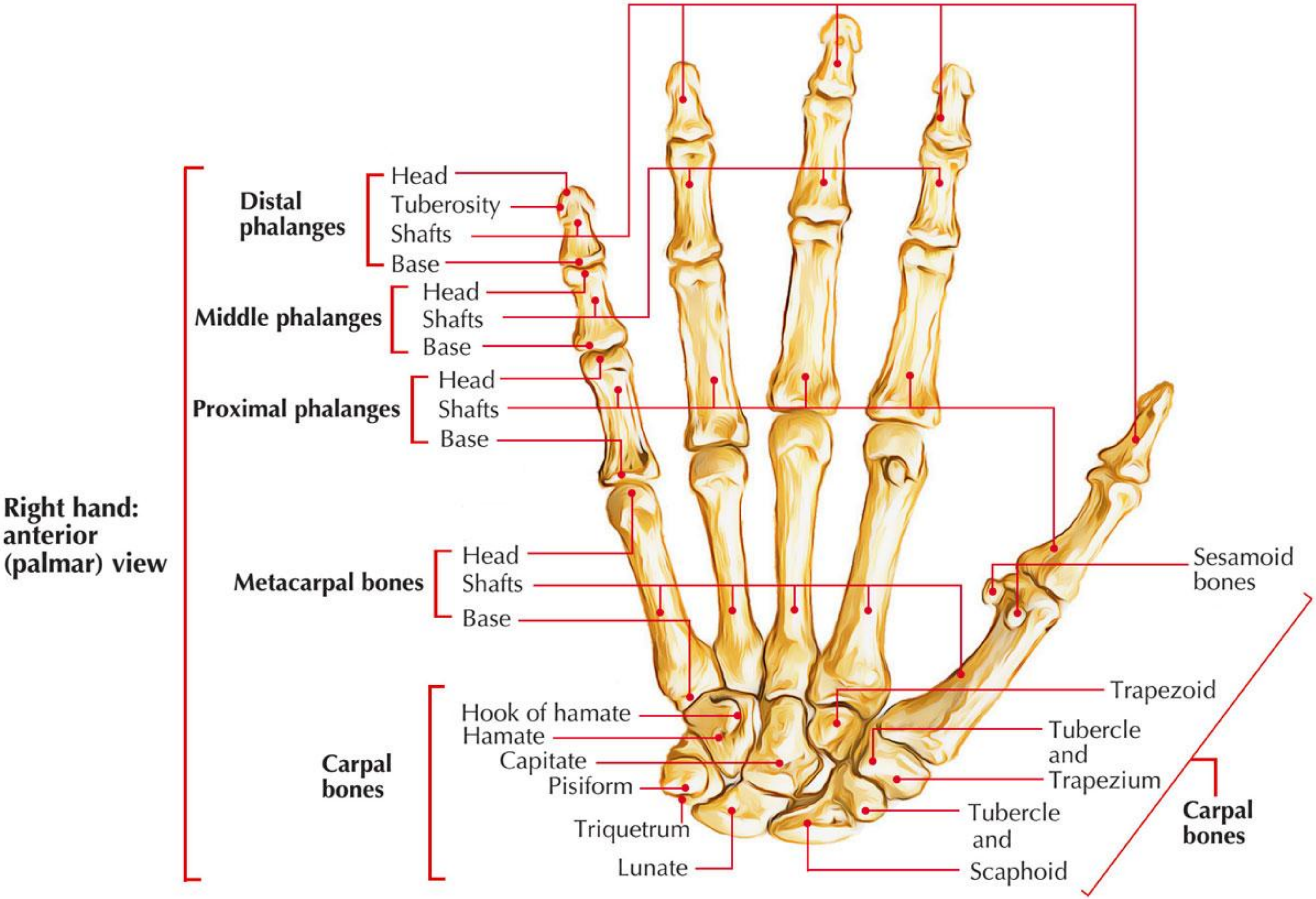
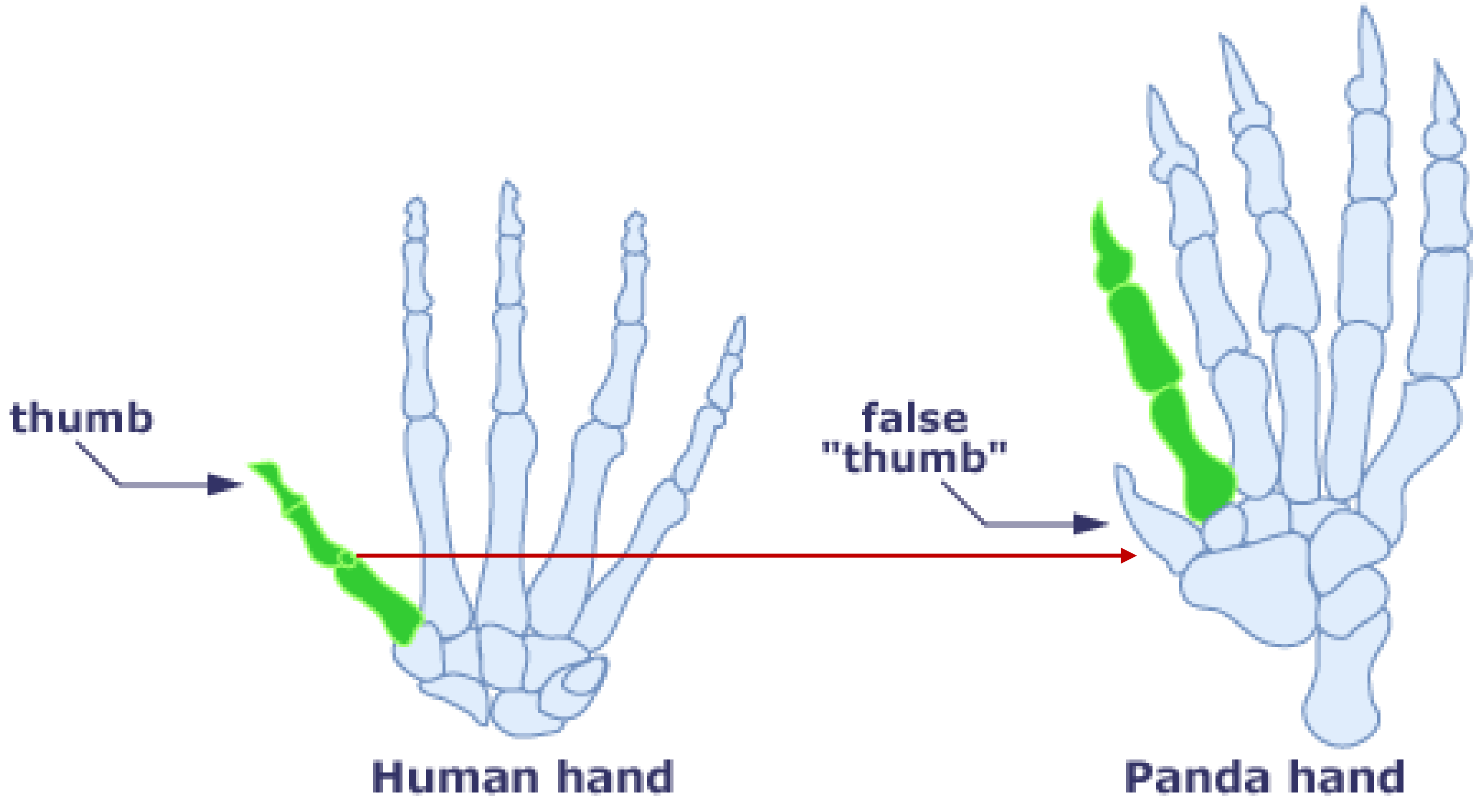
Pisiform
Sesamoid Bone
Metatarsus
Tarsals

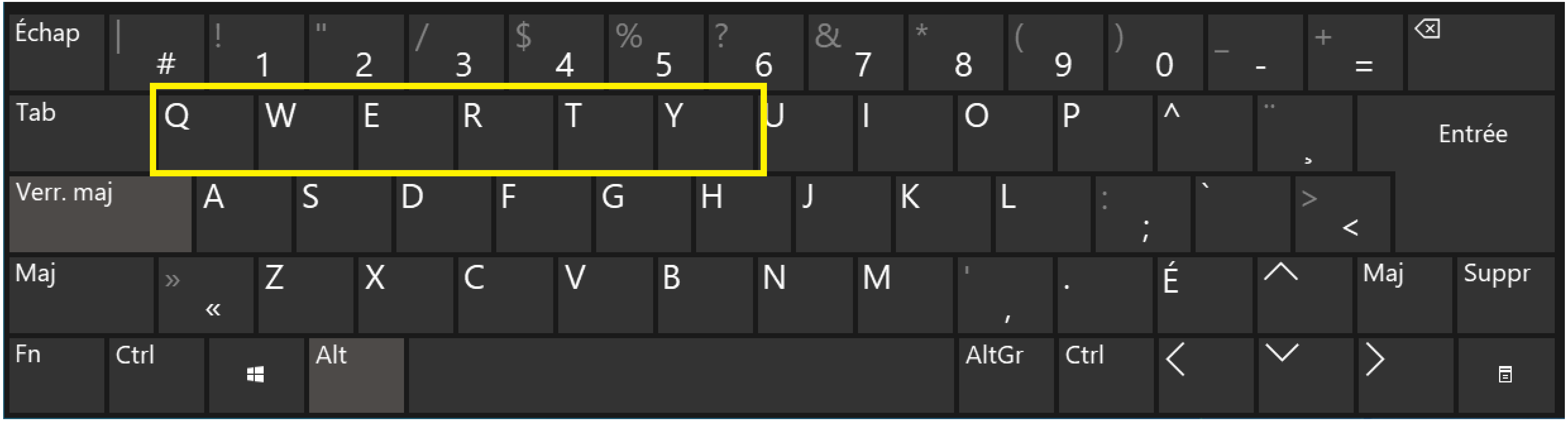

5 Fingers
Bamboo stalk
"Thumb"
"Thumb"
Radial sesamoid

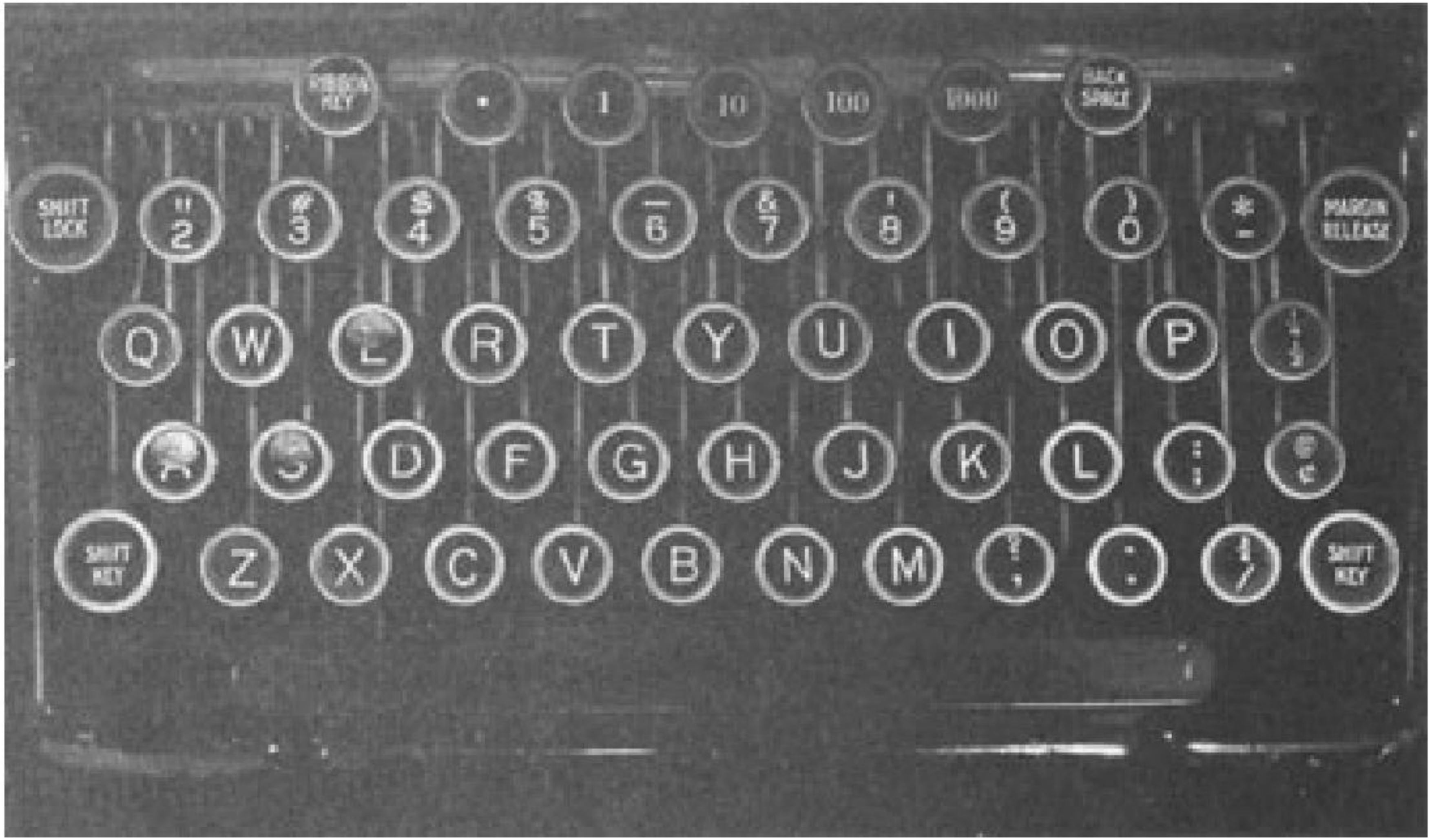

Right hand: anterior (palmar) view
Distal phalanges
Head
Tuberosity
Shafts
Base
Middle phalanges
Head
Shafts
Base
Proximal phalanges
Head
Shafts
Base
Metacarpal bones
Head
Shafts
Base
Carpal bones
Hook of hamate
Hamate
Capitate
Pisiform
Triquetrum
Lunate
Sesamoid bones
Trapezoid
Tubercle and Trapezium
Tubercle and Scaphoid
Carpal bones

Maladaptive (or non-adaptive) traits can hitchike others. Not all traits are «optimal» in a species!

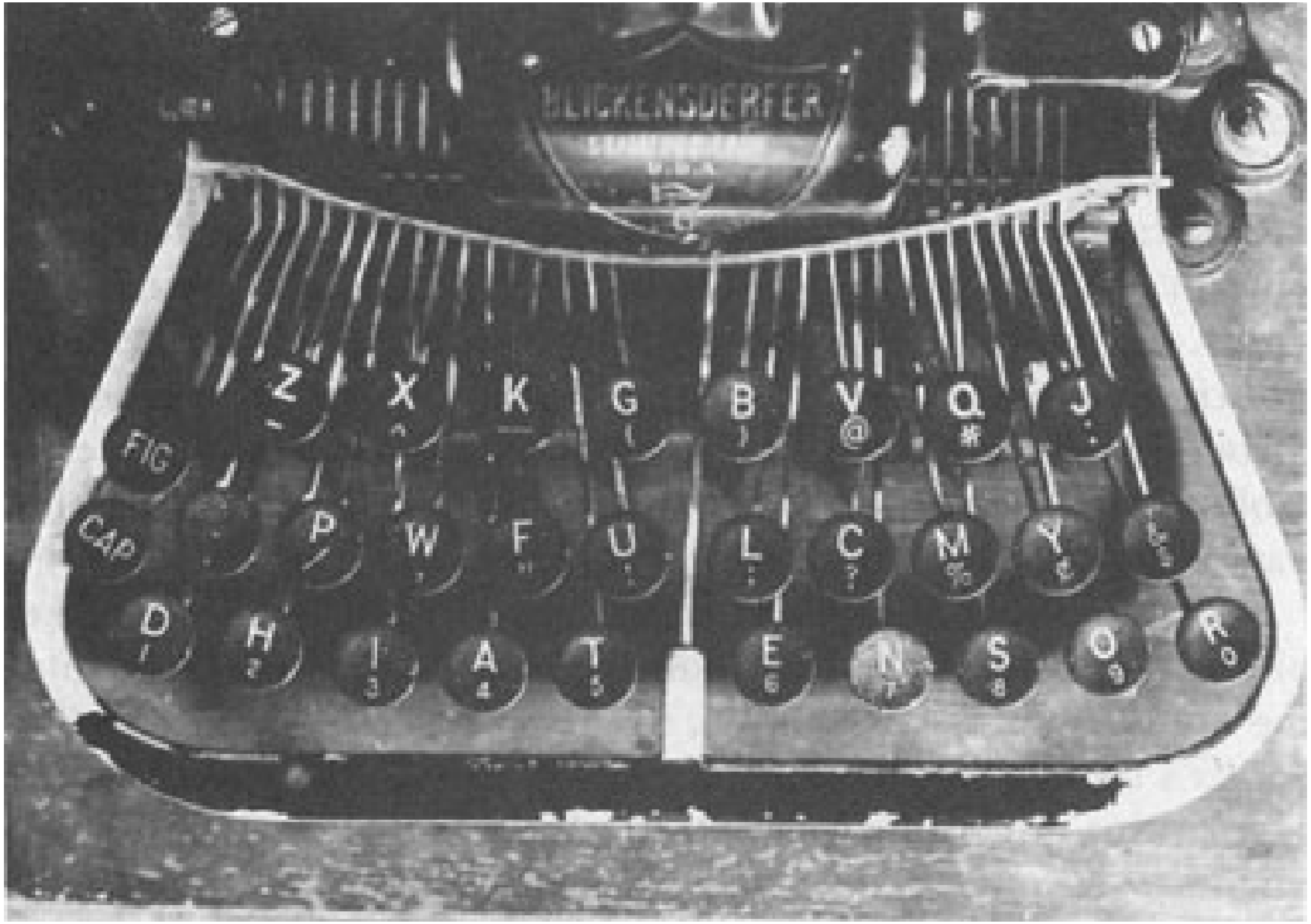


4 | The Panda's Thumb of Technology

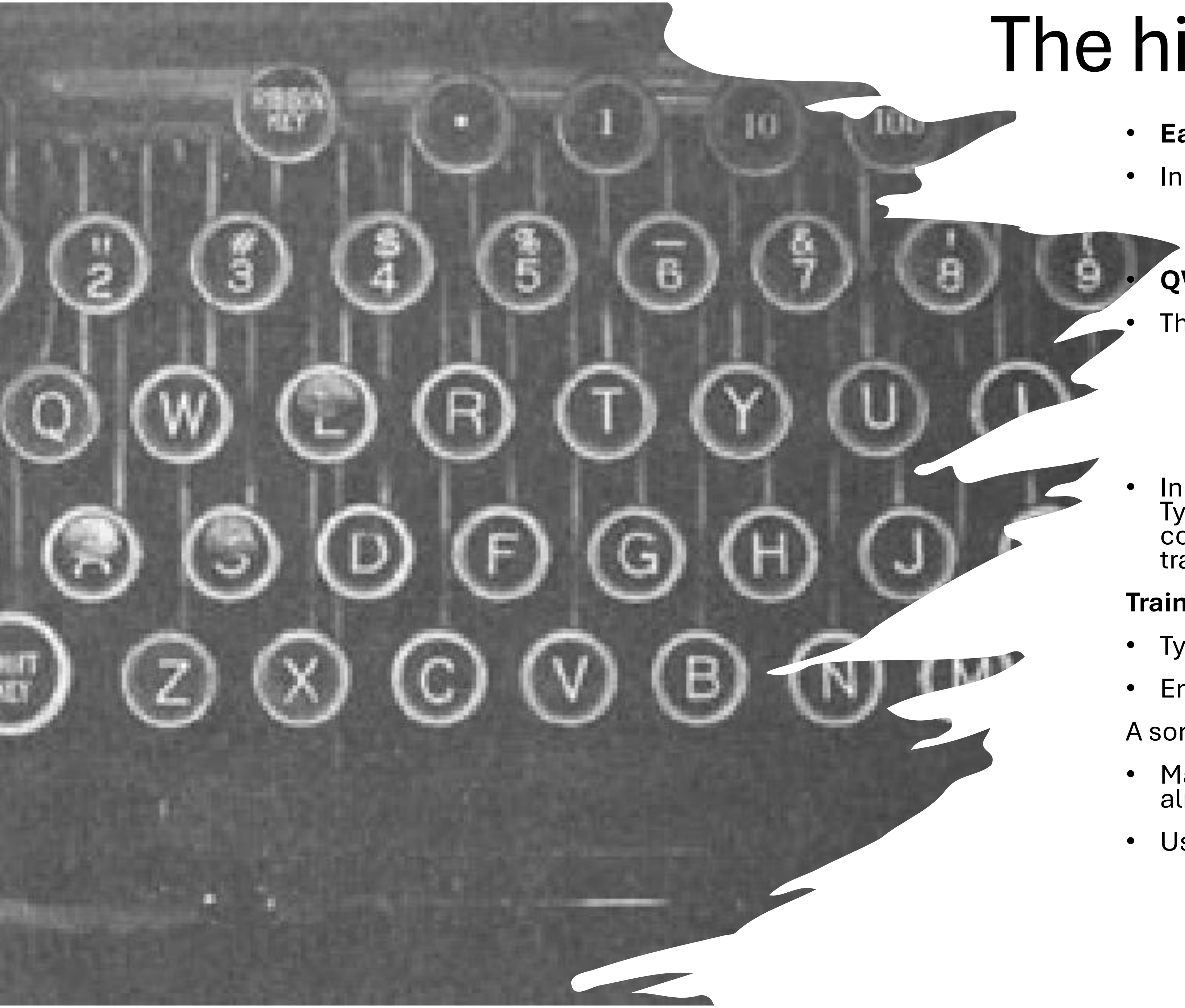




The most common letters are A, S and E. Why then A has to be typed with the ring finger? And why so much to do on the left hand?



A keyboard for a typewriter made in the 1880’s, illustrating one of the many competing non-QWERTY arrangements so common at the time.



The history of keyboards

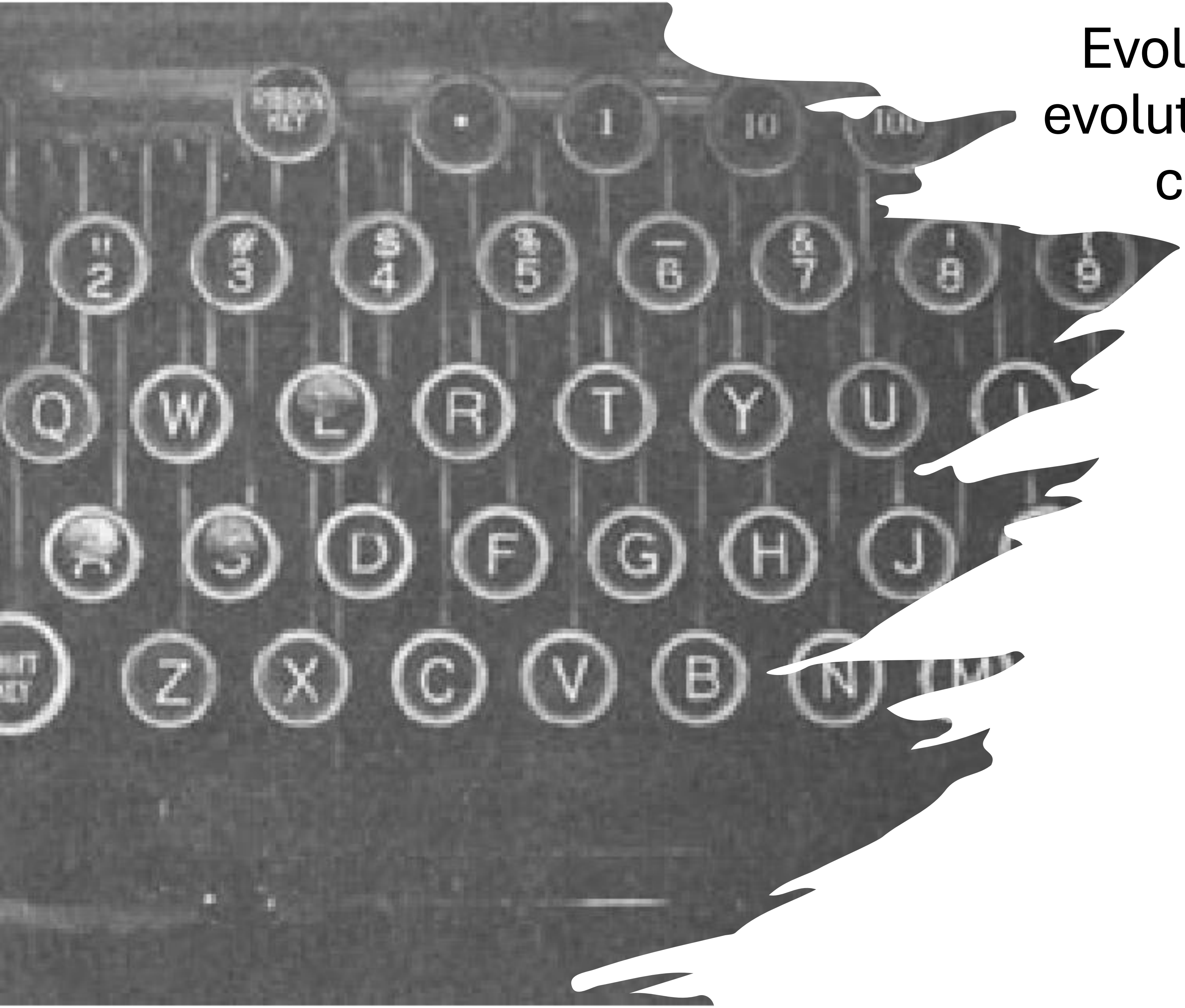
- **Early typewriters had a technical problem**
- In early mechanical typewriters:
  - Keys were connected to metal arms (“type bars”)
  - If nearby keys were struck quickly → **bars jammed**
- **QWERTY was designed to *reduce jamming***
- The layout:
  - separates commonly used letter pairs
  - slows down typing slightly
  - It gets adopted early (Remington machines)
  - In the 1880s there are still competing layouts
- In 19888 Ms Longley, founder of the Shorthand and Typewriter Institute of Cincinnati organized a typing competition. The winner was Frank E. Gurrin, who trained on a Remington QWERTY typewriter.

Training creates lock-in

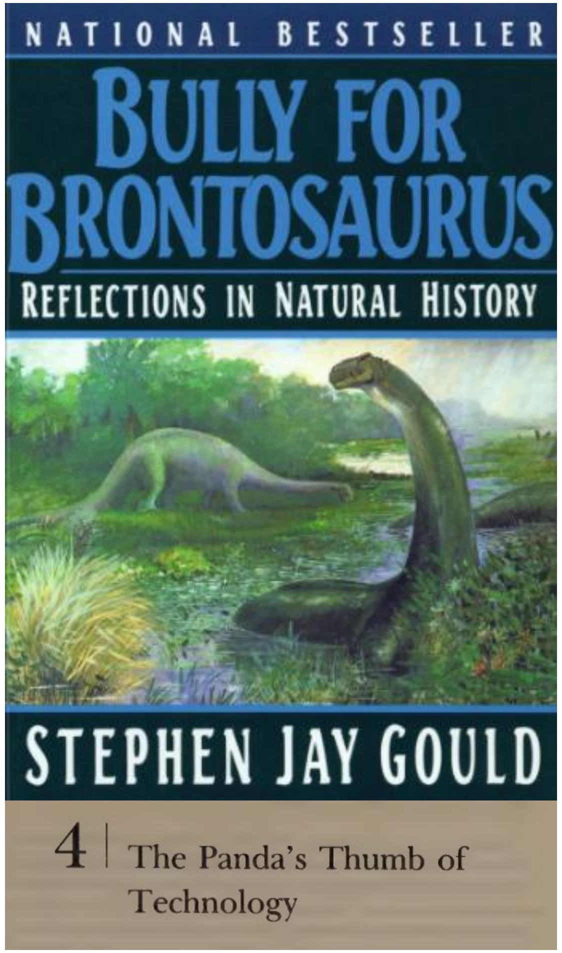
- Typists learn QWERTY
- Employers hire QWERTY-trained typists

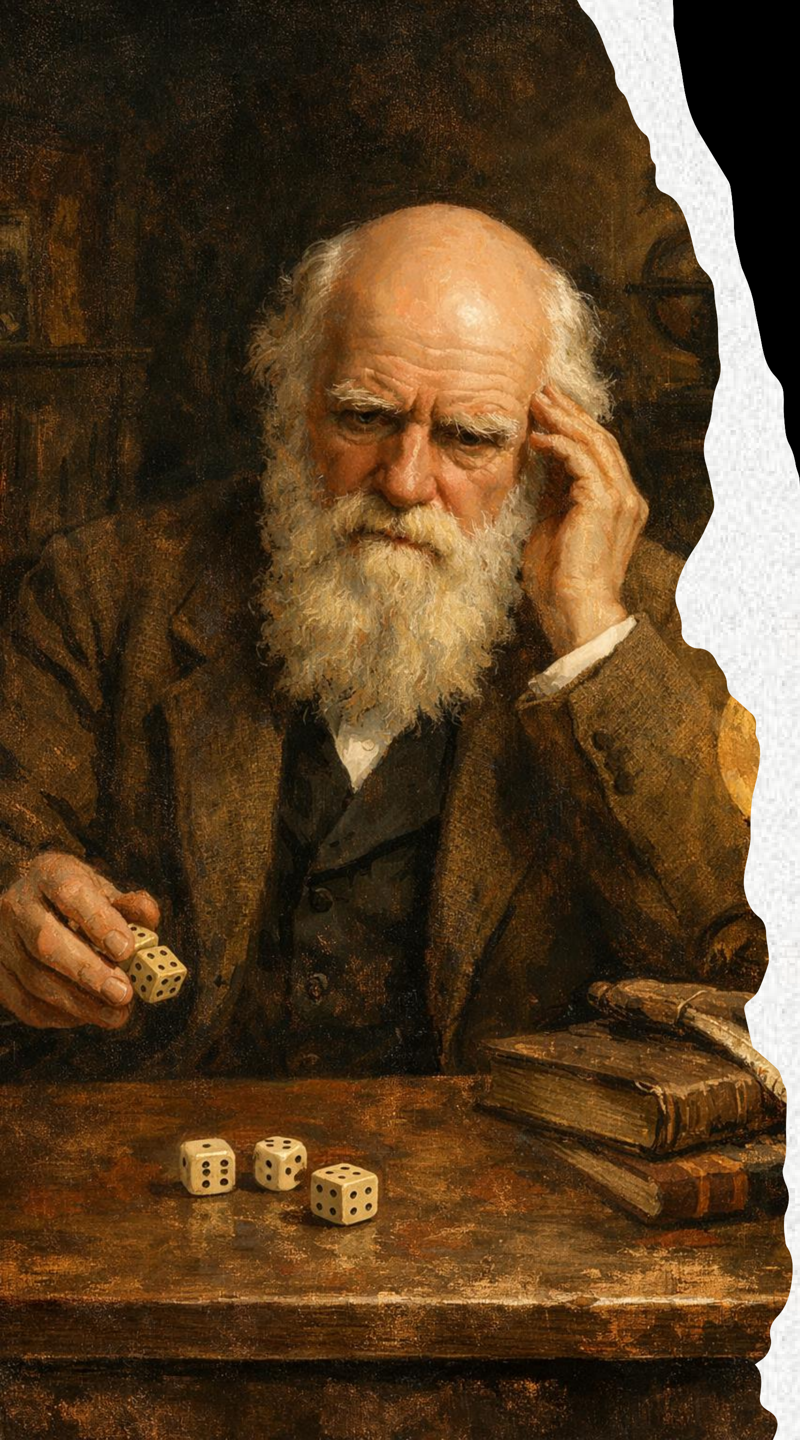
A sort of “Nash equilibrium”:

- Manufacturers stick with QWERTY because users already trained!
- Users stick with QWERTY because machines use it!



Evolution (including cultural evolution) does not «optimize»: contingency matters!!





To paraphrase Einstein..

«God does not play dice, but Darwin does»

Evolution (including cultural evolution) does not «optimize»: contingency matters!!

Types of environmental change

Temporal mode:

- **Gradual**
  - If very gradual, directional selection
  - The possibility to adapt depends on the pace of change
- **Abrupt**
  - Response is usually just extinction
- **Uncertain**
  - Bet-hedging
  - Plasticity and learning

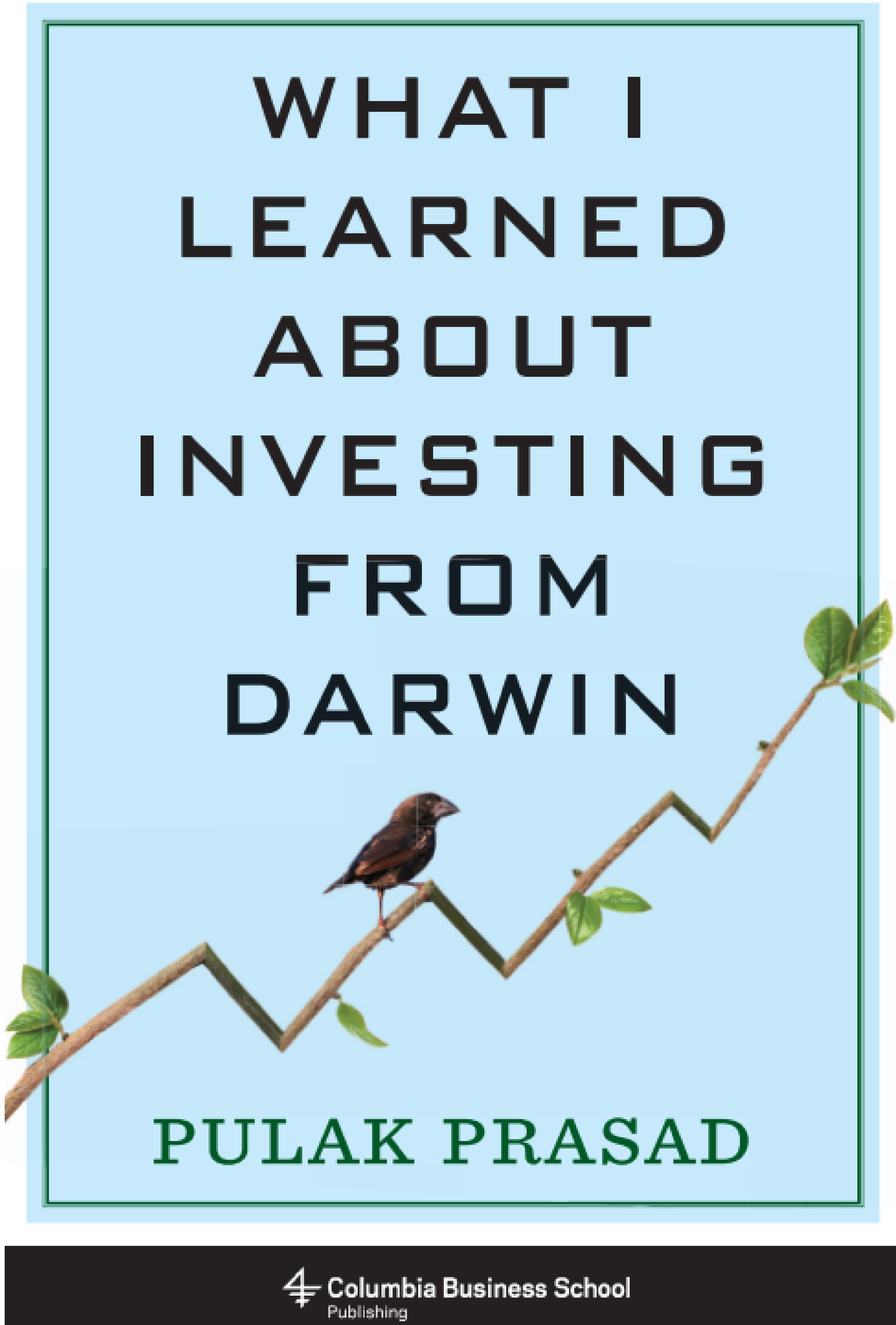
Uncertainty

Stochastic «unforeseeable» environmental fluctuations, either:

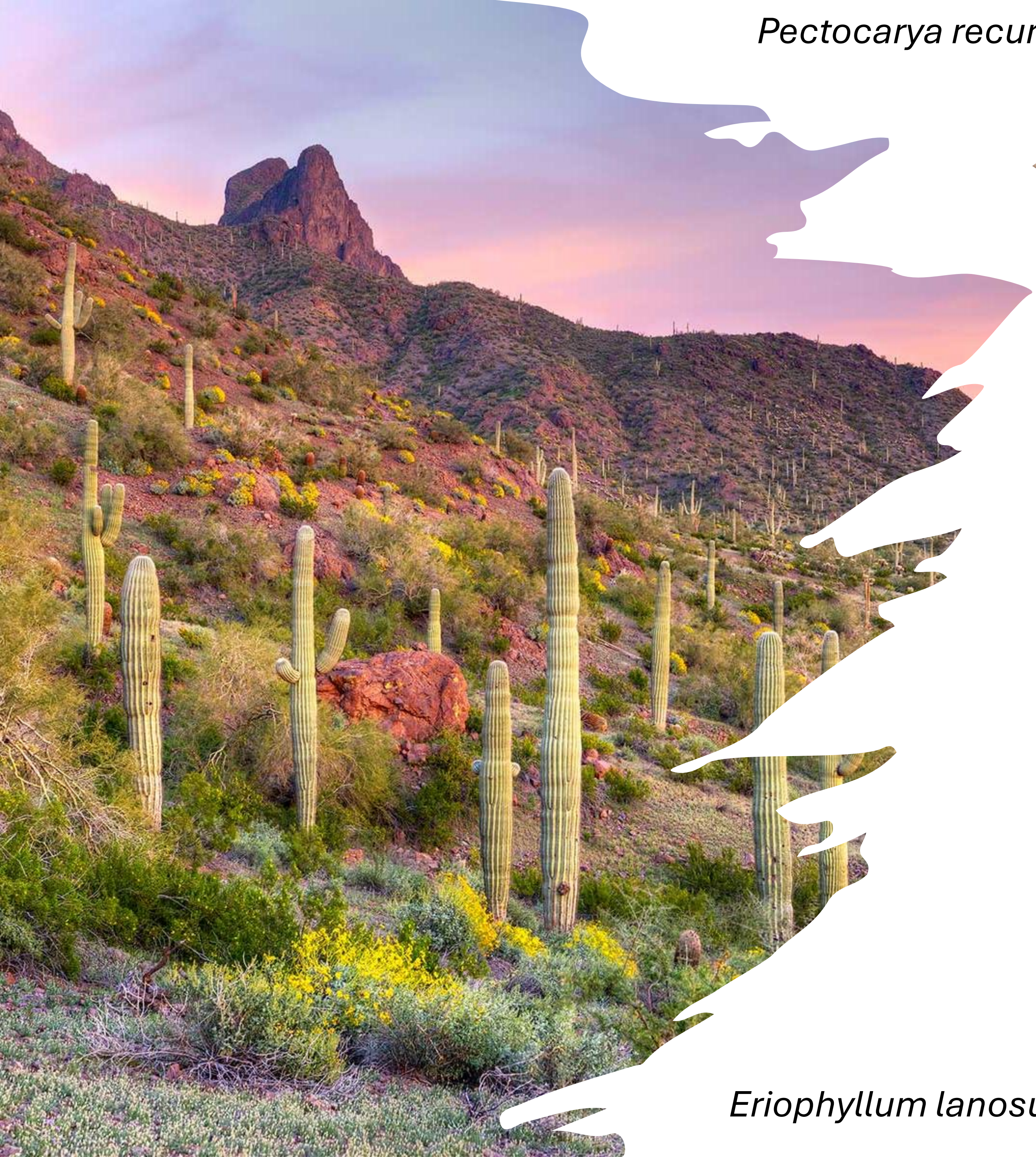
- Aggregate: affecting all individuals in a population
- Idyosyncratic: affecting only one or few individuals

Examples:

- Weather (rainy years, drought, etc.)
- Ecological (presence or absence of competitors or predators)
- Etc.




Sonoran desert



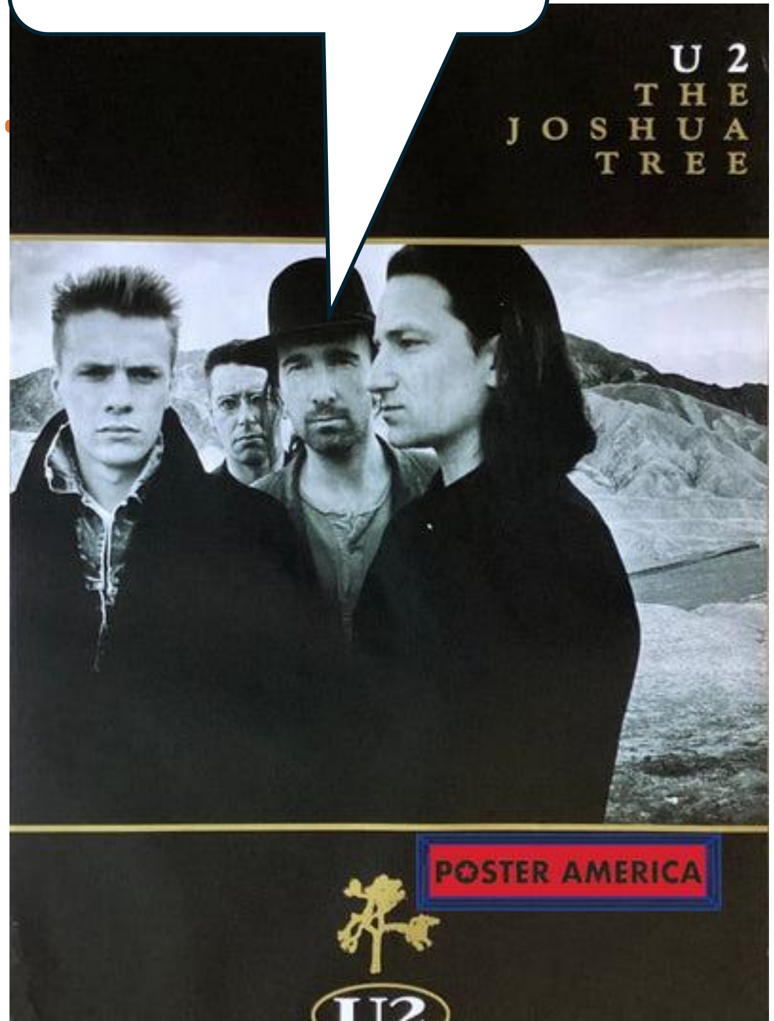
Pectocarya recurvata

Eriophyllum lanosum

Negev desert

Anastatica hieronchutica

We should have made a song about ***Linanthus parryae*** *too*



What strategy would you choose?

Let's assume that 60% of the times it is a wet-year

	Wet year	Drought
Germinate	4	0
Dormancy	1	1

Strategy with maximum short term payoff?
Germinate:
Dormancy:

What strategy would you choose?

Let's assume that 60% of the times it is a wet-year

	Wet year	Drought
Germinate	4	0
Dormancy	1	1

Strategy with maximum short term payoff:
Germinate: 4*0.6+0=2.4 *V*
Dormancy: 0.6

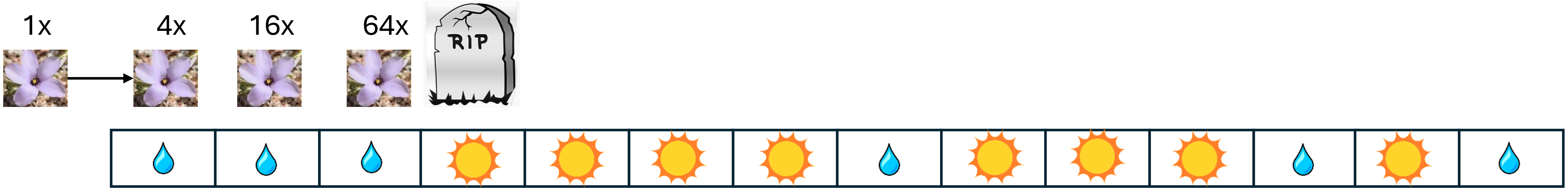
What happens if the seed always choose the strategy giving the highest short-term payoff?

1x

→ ?

	Wet year	Drought
Germinate	4	0
Dormancy	1	1

What happens if the seed always choose the strategy giving the highest short-term payoff?



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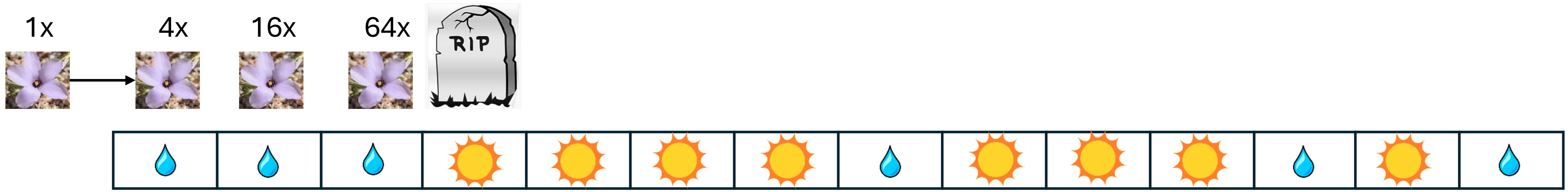
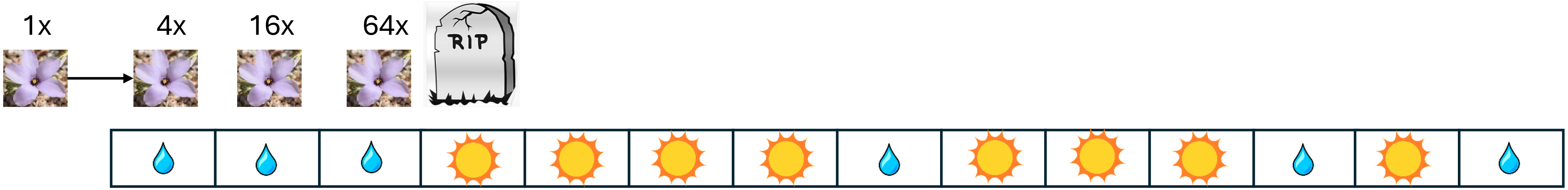


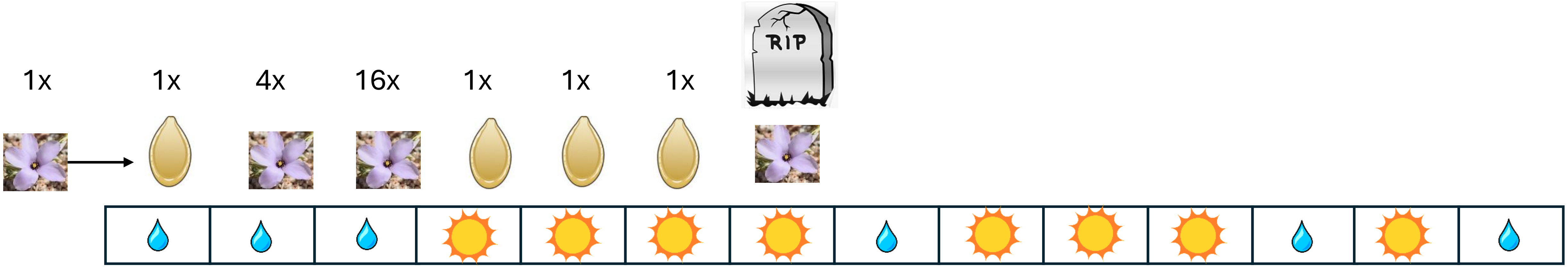
Solution?

	Wet year	Drought
Germinate	4	0
Dormancy	1	1

Always germinate (Maximizing short term payoff)

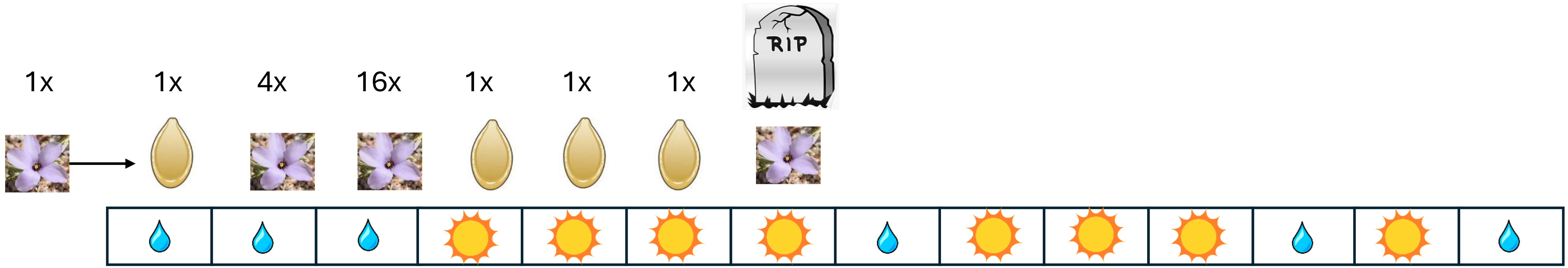


Bet-hedging/phenotype-switching (50% germinate, 50% dormancy)



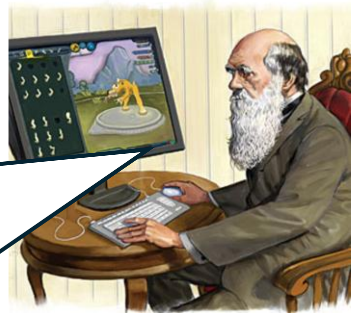
What is the best bet-hedging strategy?

Bet-hedging/phenotype-switching (50% germinate, 50% dormancy)



What is the best bet-hedging strategy?

Demostrate this at home (with example or intuitive proof). But when it is live or die situation, the fittest probability of dormancy match that of drought (so if it rasin 60% of the years, a seed should germinate 60% of the times)



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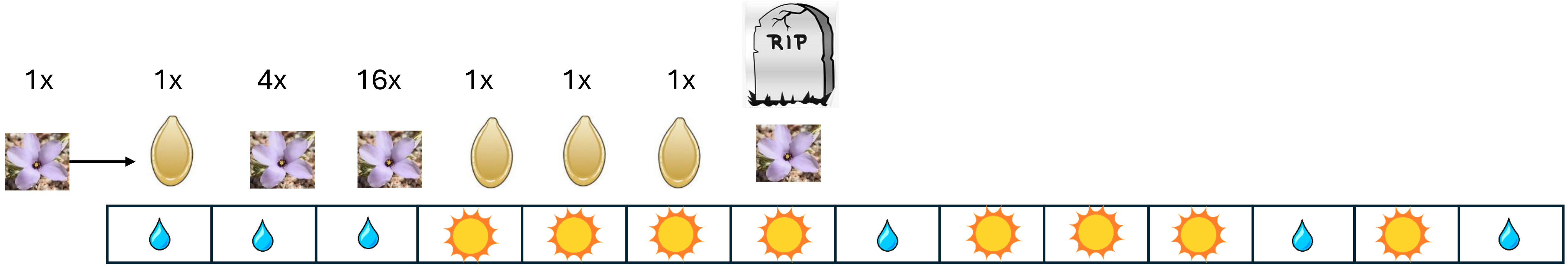
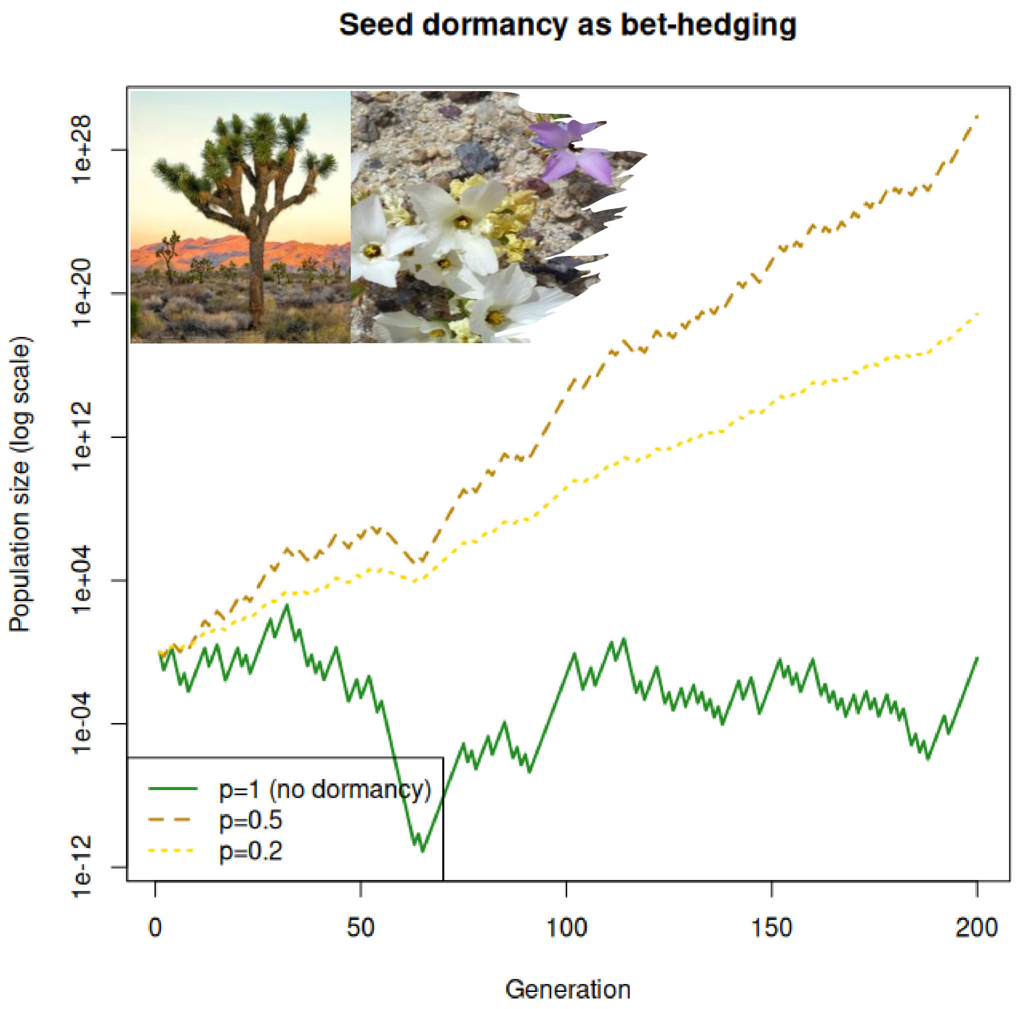


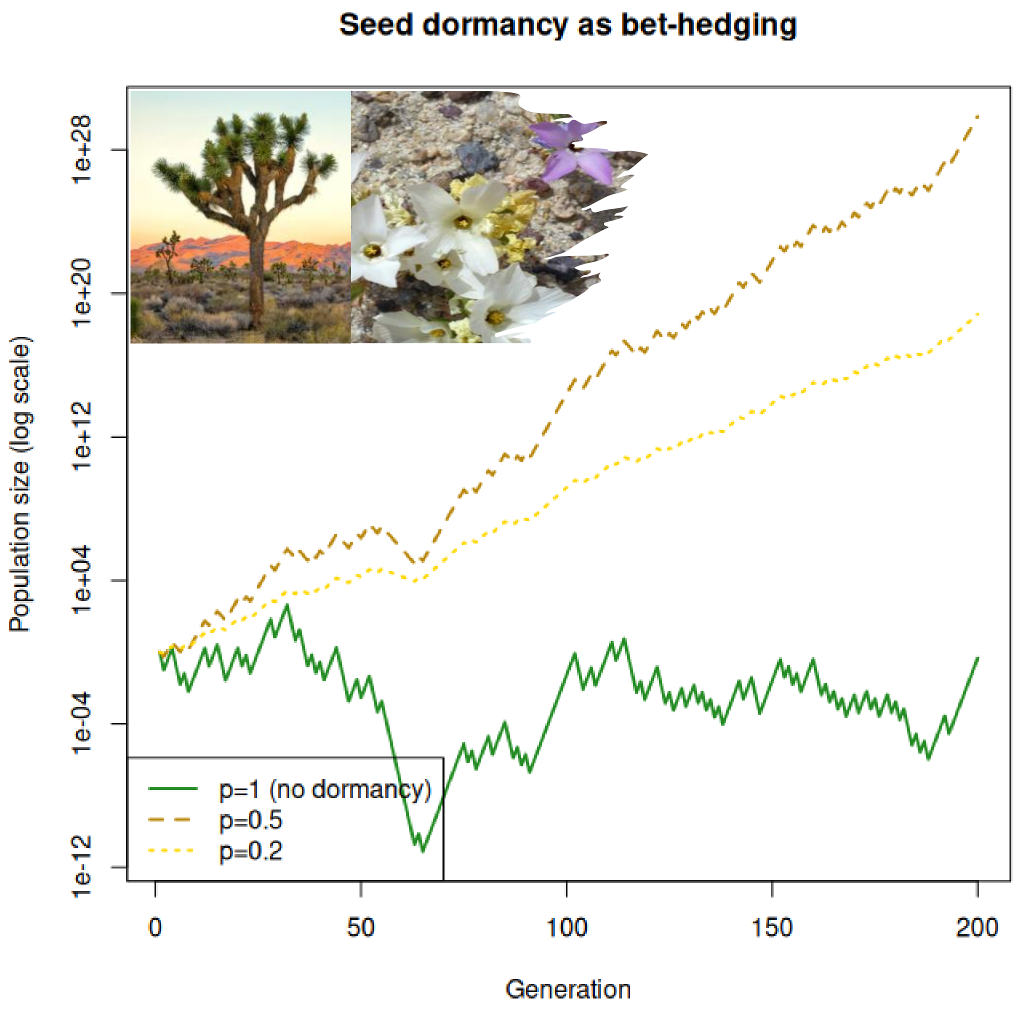
Sonora-like desert



Probability of rain/good year=60%

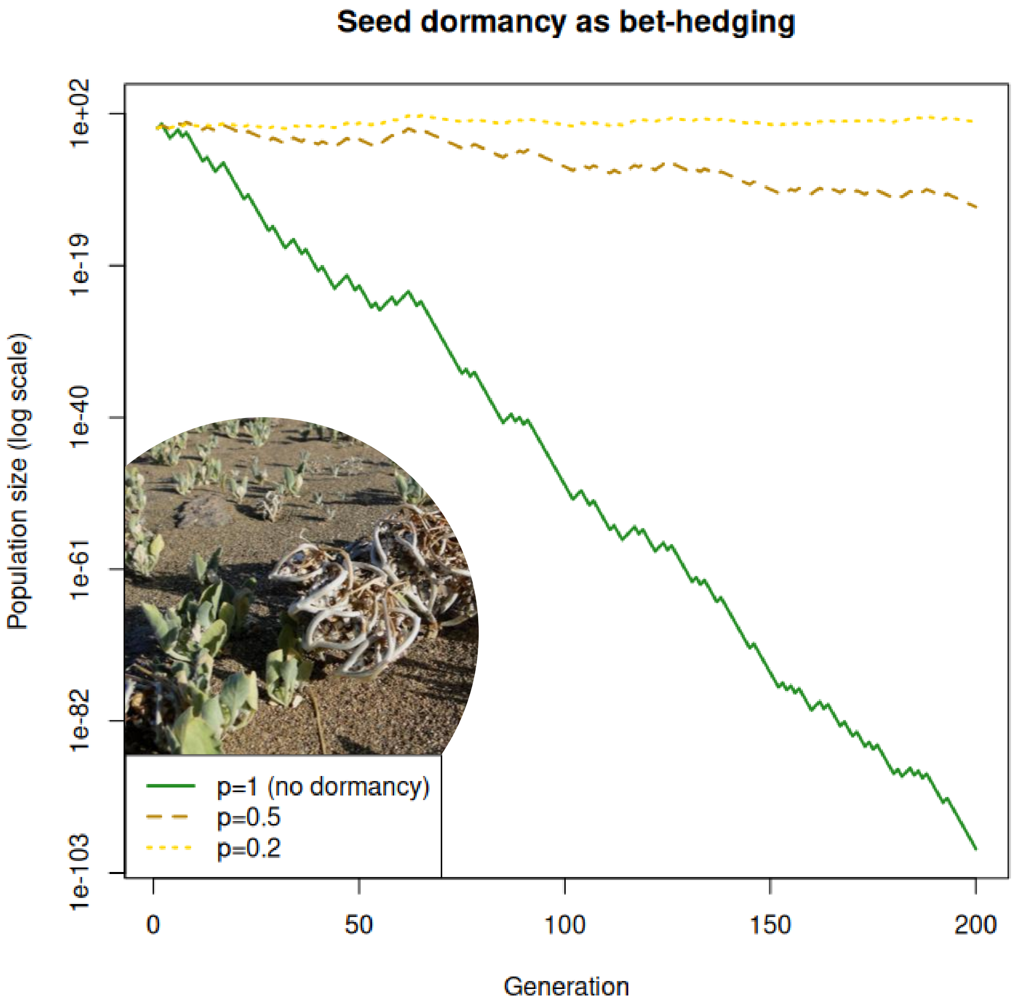
	Wet year	Drought
Germinate	4	0.1
Dormancy	1	1

Sonora-like desert



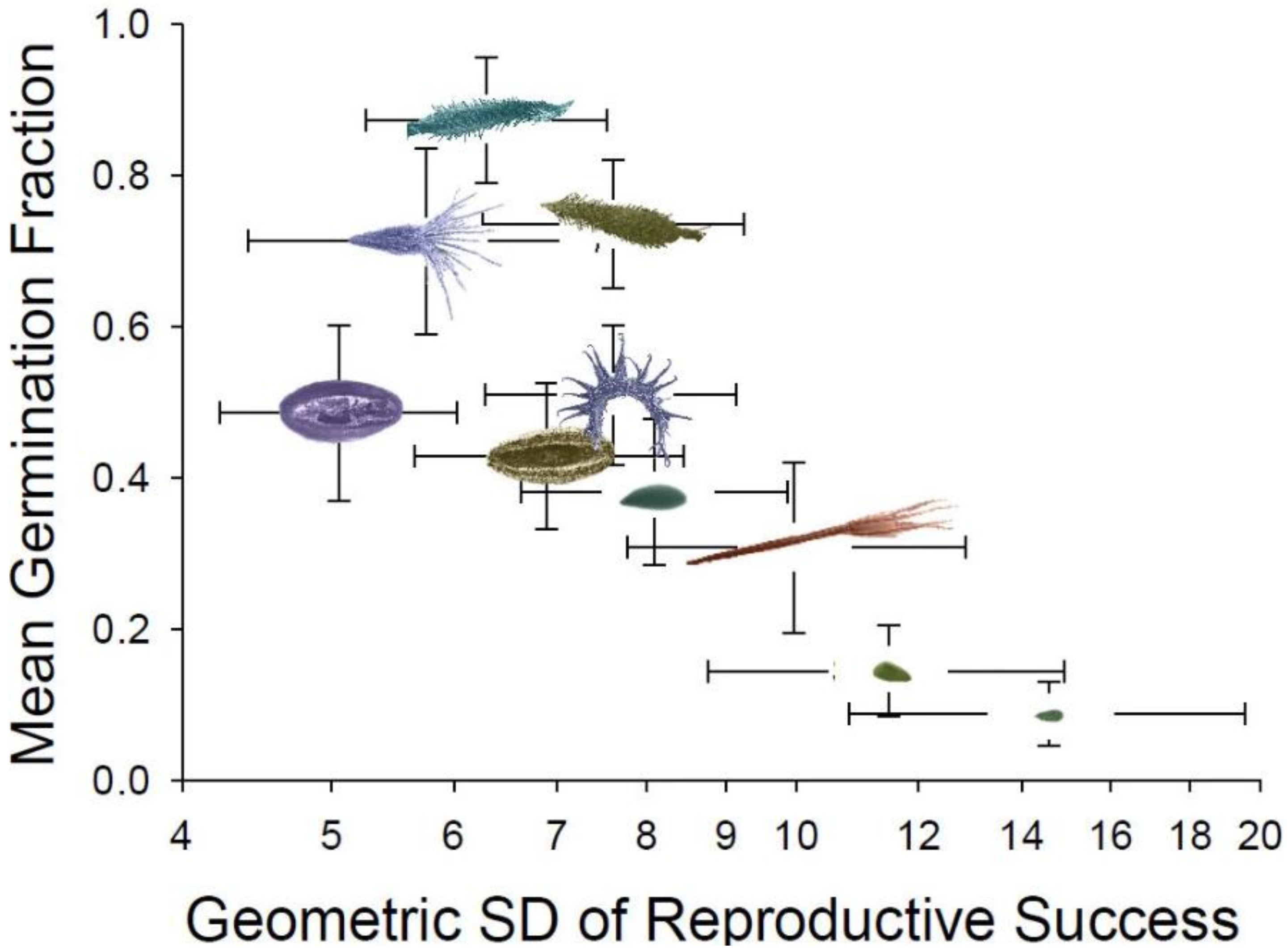
Probability of rain/good year=60%

Negev desert



Probability of rain/good year=30%

It is empirically observed that germination rates match predictions



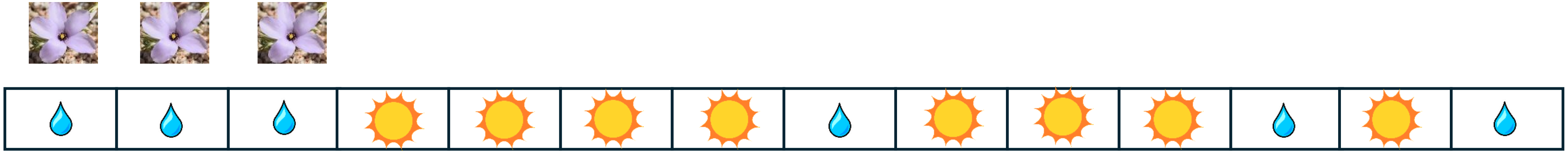
[Desert lab]

If evolution is not «maximizing» short-term fitness, what is it «selecting for»?

	Wet year	Drought
Germinate	2	0
Dormancy	1	1

Additive fitness

Fitness: 2 + 2 + 2 + 0 + 0 + 0 + 0 + 2 + 0 + 0 +0 +2 +0 +2 =12



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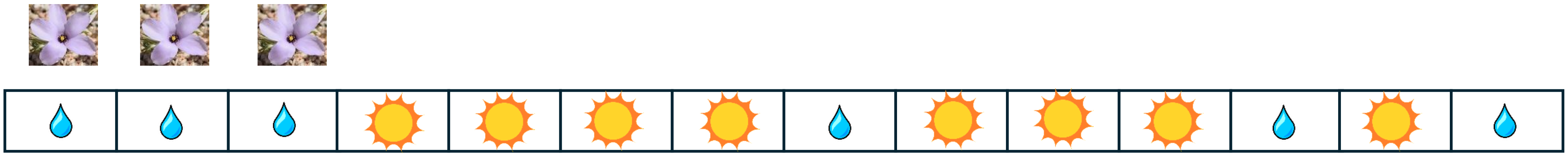
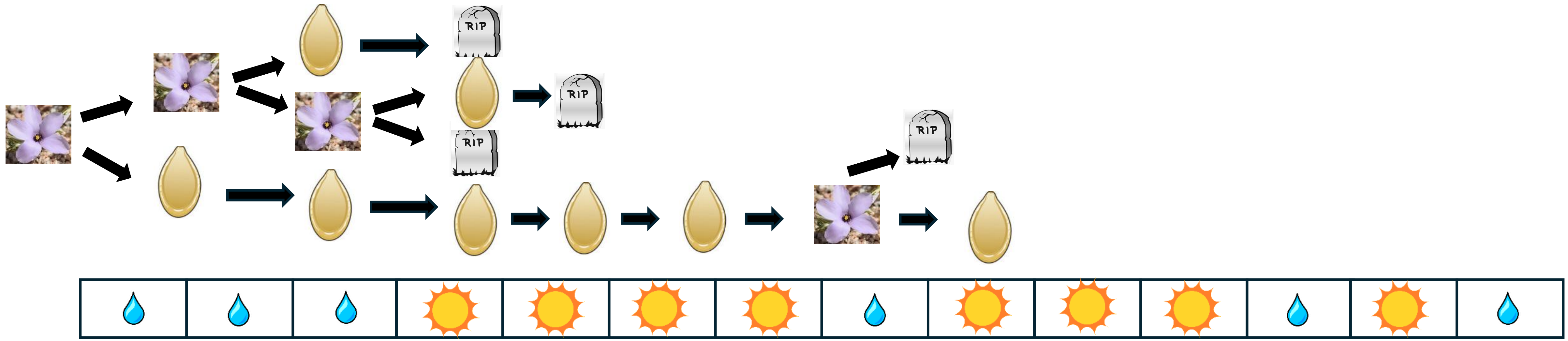


Reproduction (geometric fitness)



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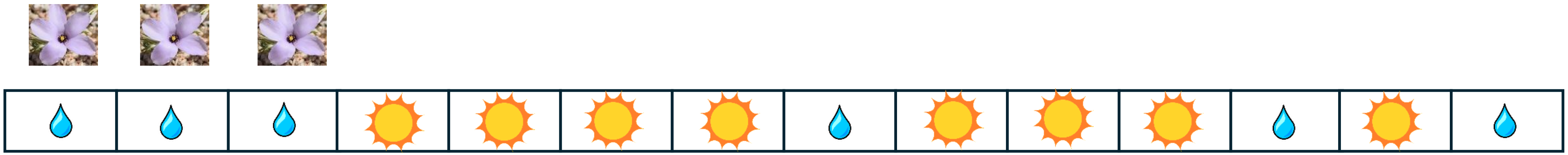

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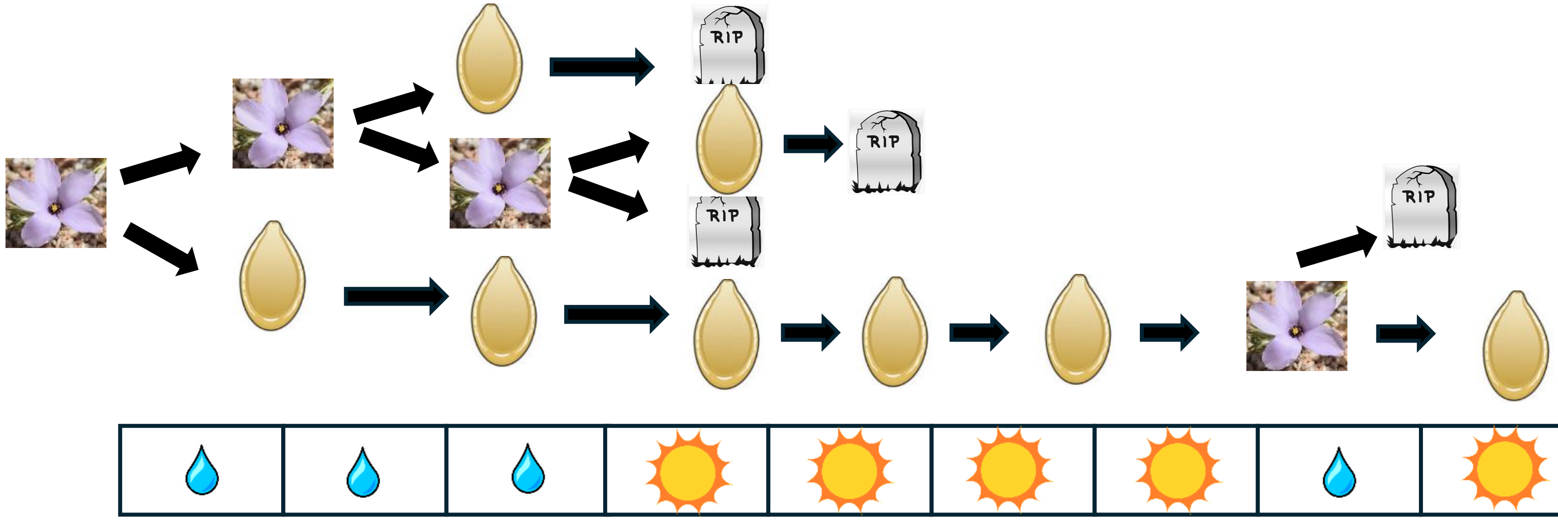
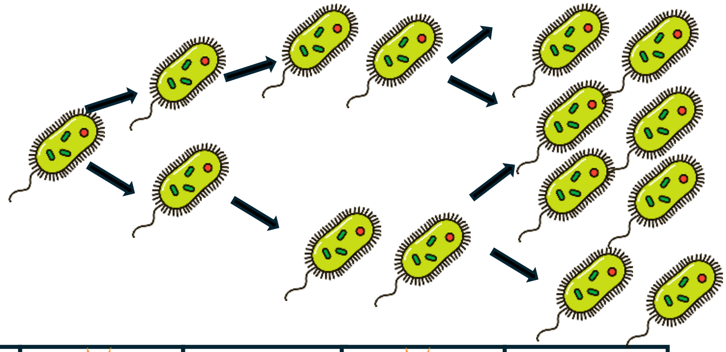


Think of it as bacterial replication!
It is not just a sum, it is a multiplication!



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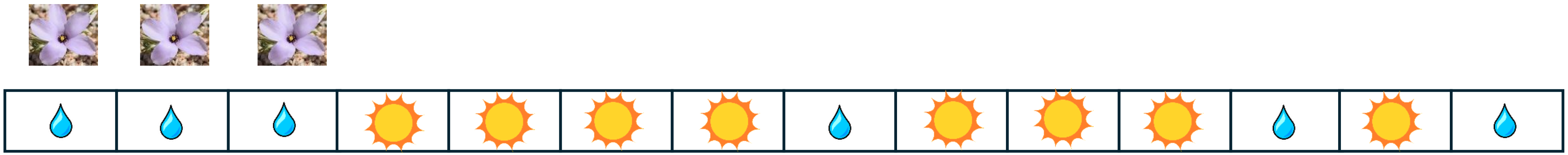
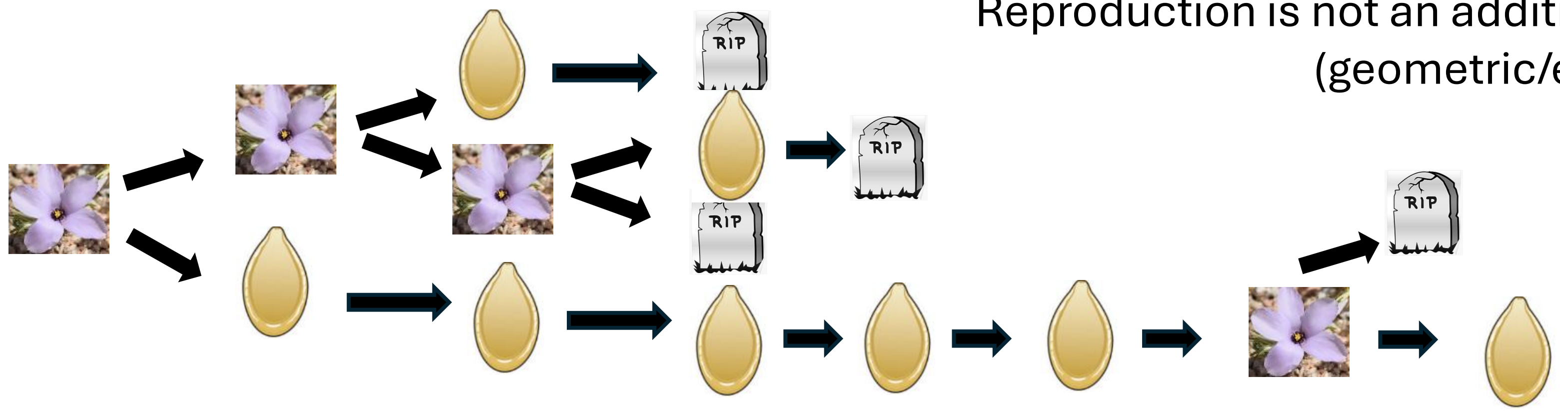


Reproduction (geometric fitness)

Reproduction is not an additive process, but a ***branching*** process! (geometric/exponential process)!



Each offspring gives birth to more offspring

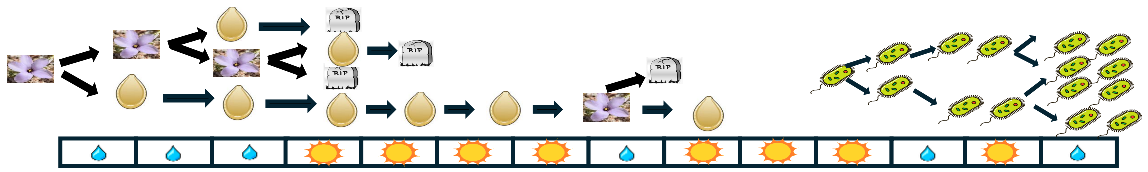
Since reproduction is «exponential», natural selection in uncertain environments maximizes «geometric fitness»/minimize variance in fitness

- Additive fitness (e.g. In a single lifetime, one offspring seed lives, one dies), then fitness:
  - Fitness: 1+0=1 — One lives and one dies
  - Fitness: ½+½=1 — Both have 50% of surviving

Same additive fitness!

- Geometric fitness (e.g. offsprings are «over successive generations»):
  - Fitness: 1*0=0 — One lives and one dies
  - Fitness: ½*½=1/4 — Both have 50% of surviving

The long term fitness is highest when reproduction is similar across generations (the variance is smallest)



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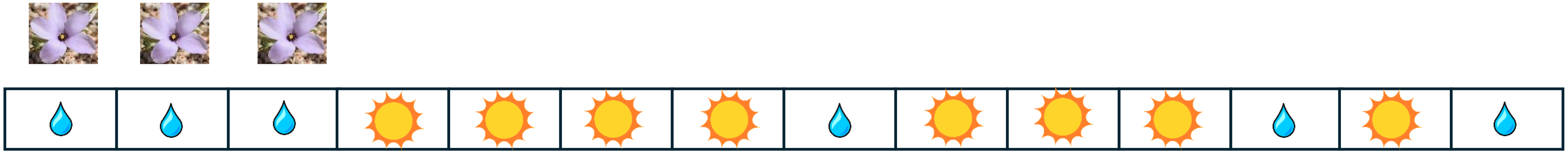
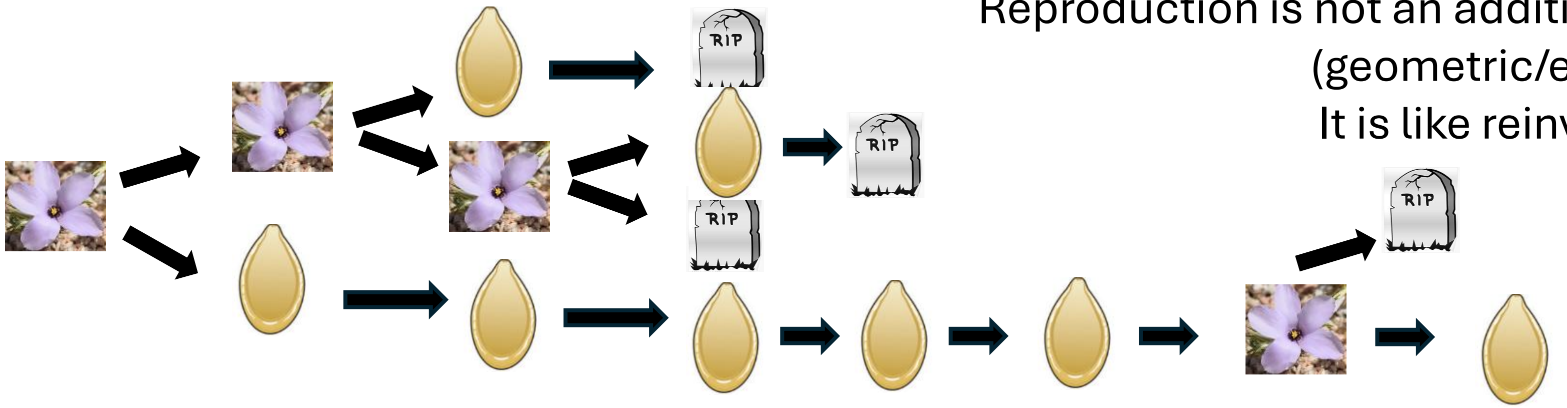


Reproduction (geometric fitness)

Reproduction is not an additive process, but a branching process!
(geometric/exponential process)!
It is like reinvesting what earned!



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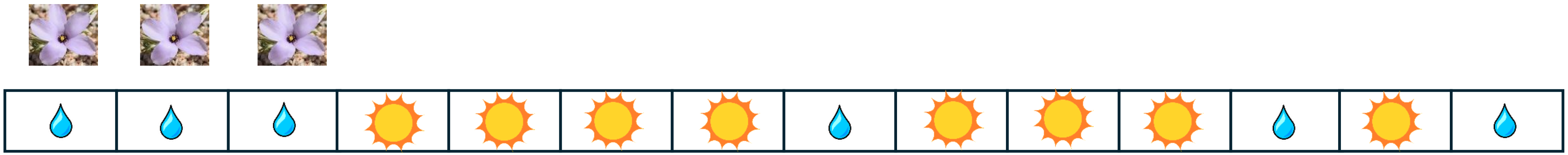

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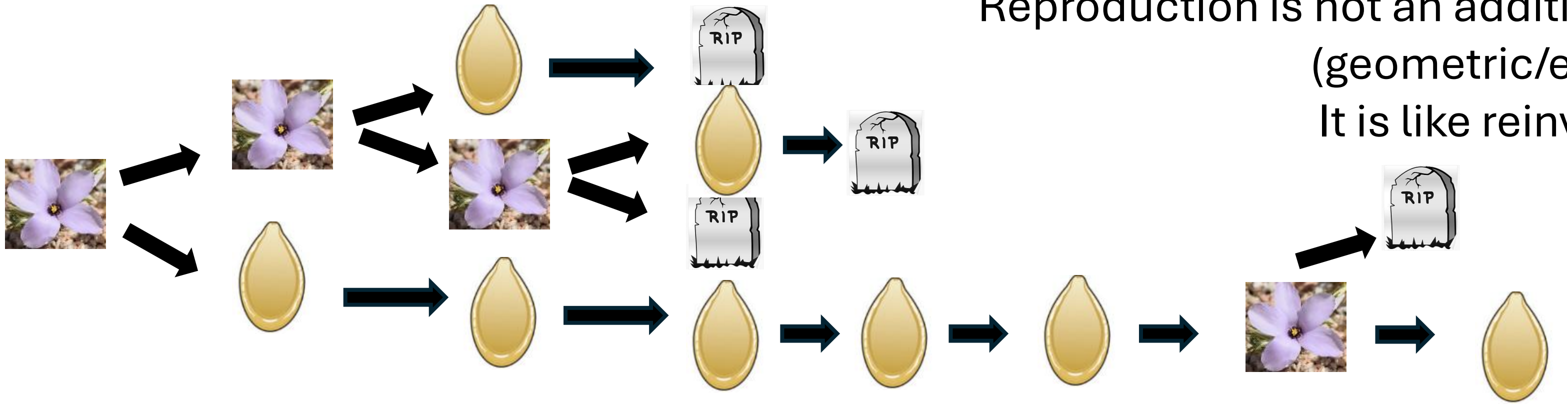
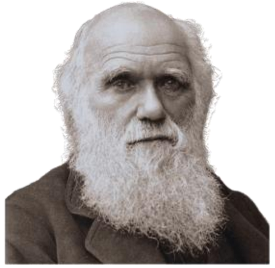


A Great Investor Is a Great Rejector

SECTION I

AVOID BIG RISKS



On the other hand, in some cases, as with the elephant and rhinoceros, none are destroyed by beasts of prey; even the tiger in India most rarely attacks a young elephant protected by its dam.

Charles Darwin, On the Origin of Species, *chapter 3, "Struggle for Existence"*

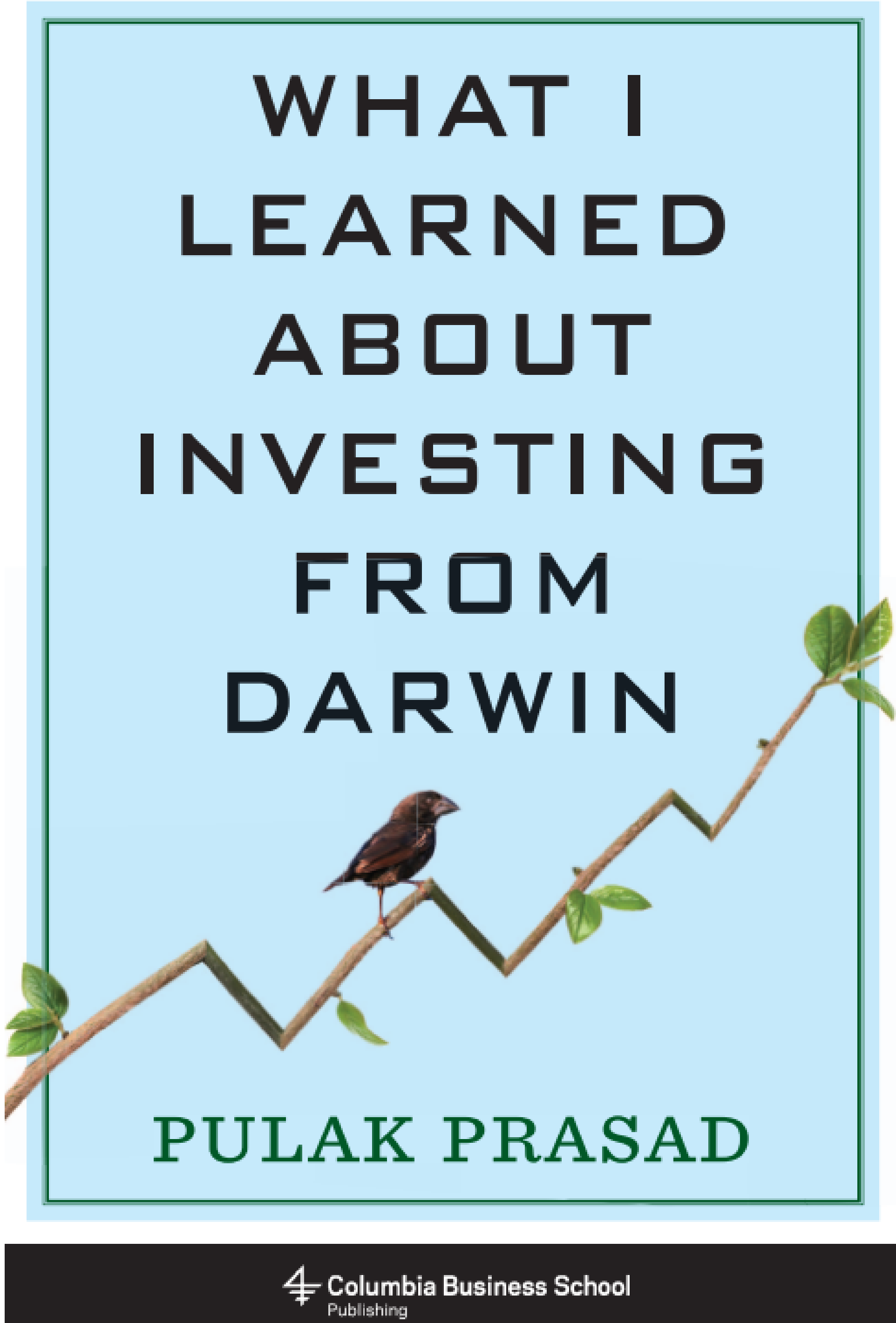
Buffett's Two Rules of Investing

As one should expect, Warren Buffett figured out this lesson from evolutionary theory before almost everyone else. He famously coined his two rules of investing as follows:

> Rule number 1: Never lose money.
> Rule number 2: Never forget rule number 1.[10]

In our view, it is folly to forgo buying shares in an outstanding business whose long-term future is predictable, because of short-term worries about an economy or a stock market that we know to be unpredictable. Why scrap an informed decision because of an uninformed guess?

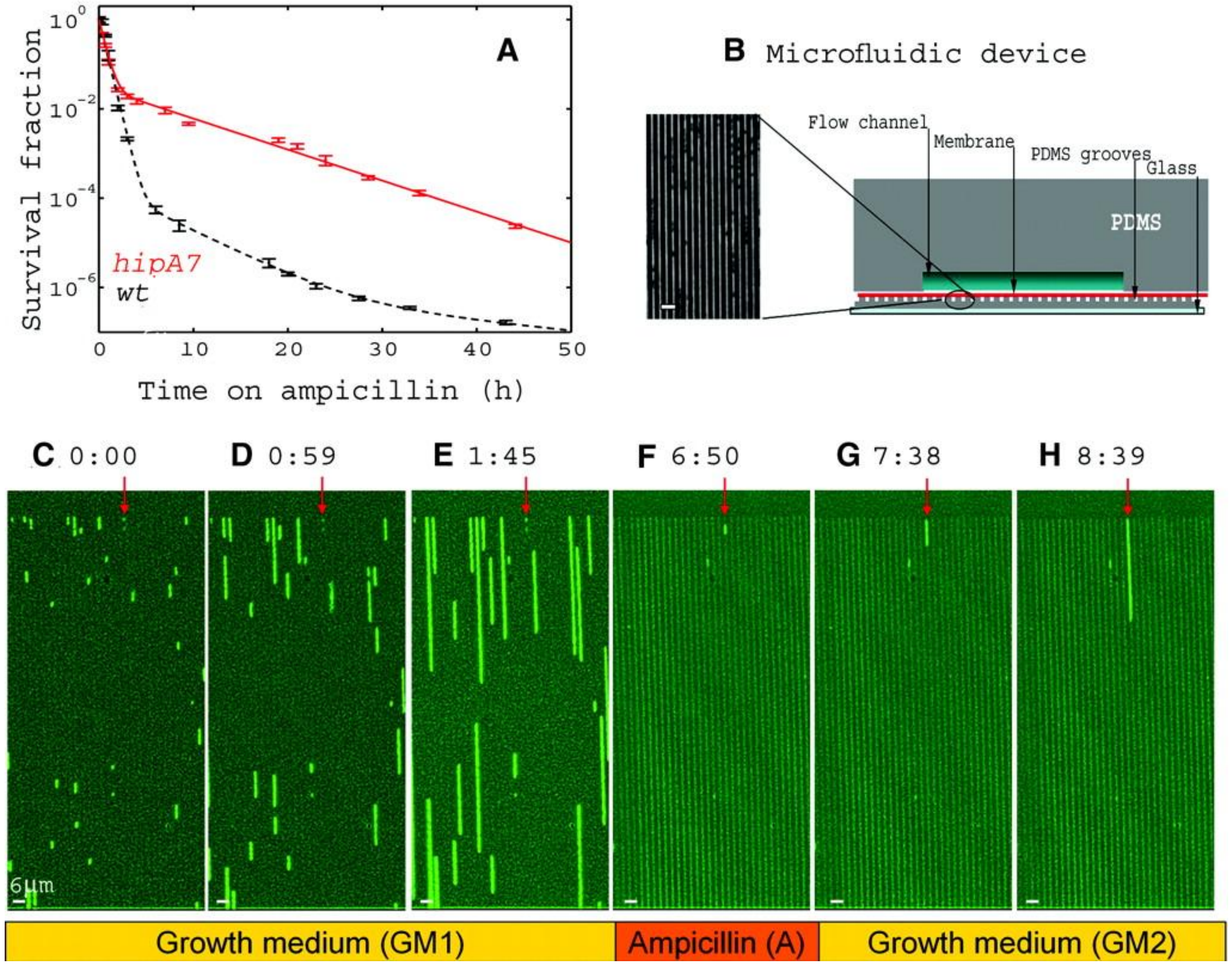
Warren Buffett, annual letter to shareholders, 1994



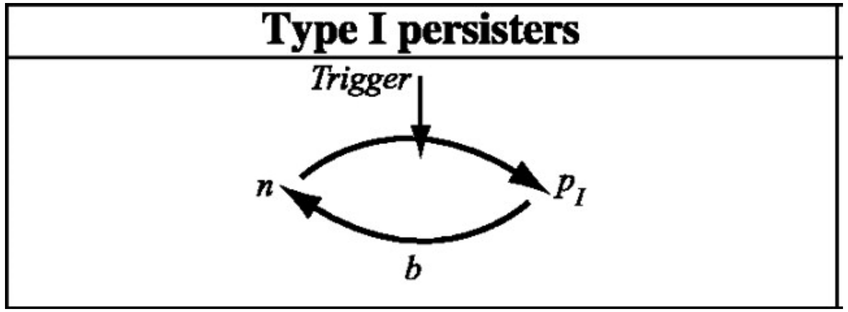
10 SEPTEMBER 2004 VOL 305 SCIENCE www.sciencemag.org

Bacterial Persistence as a Phenotypic Switch

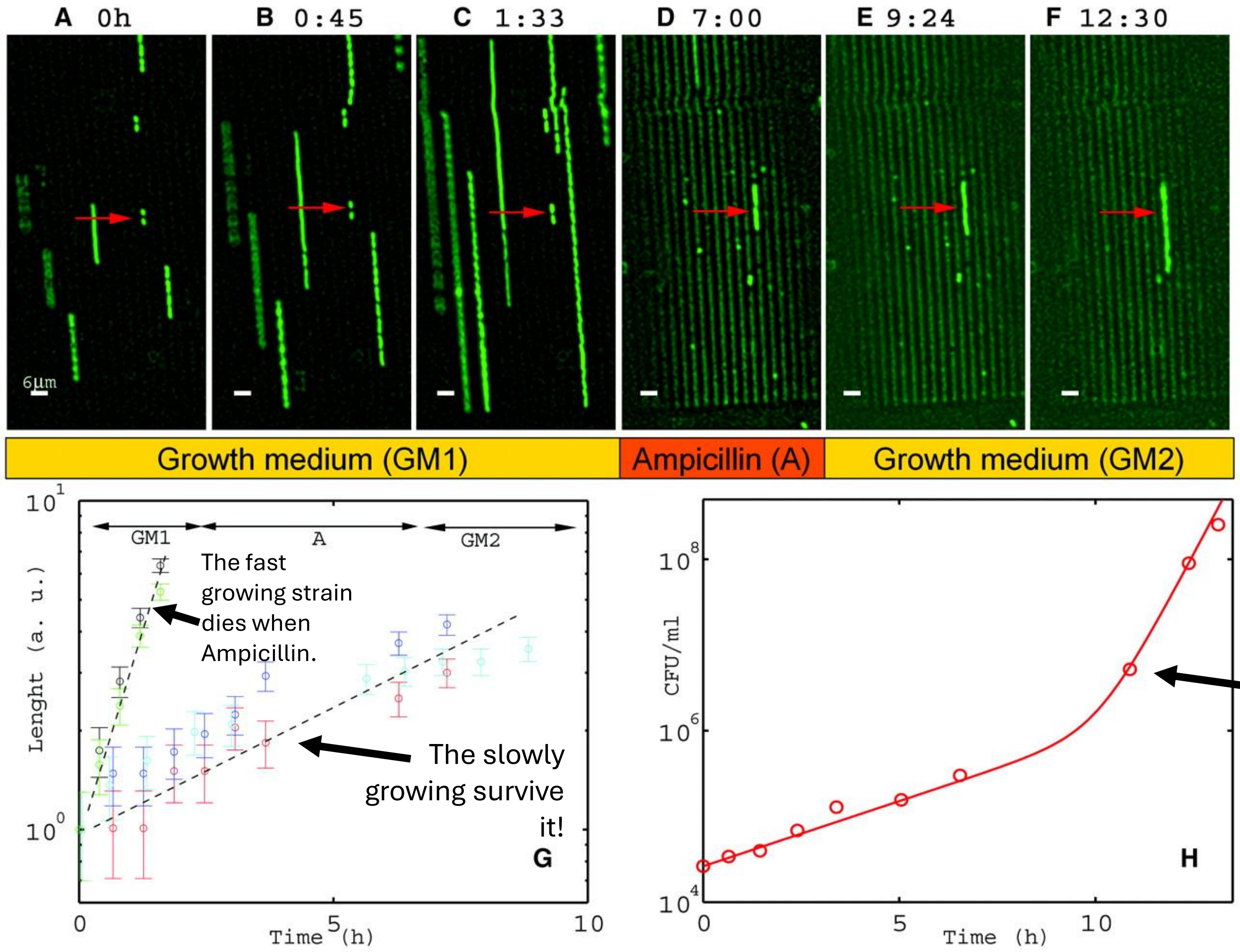
Nathalie Q. Balaban,[1,2*] Jack Merrin,[1] Remy Chait,[1]
Lukasz Kowalik,[1] Stanislas Leibler[1]



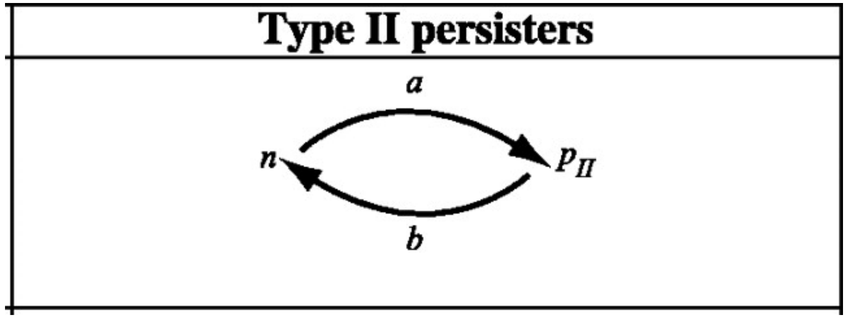
Type I switching (induced upon a trigger): *hipA7* mutan



Bacterial resistance to stress and antibiotic also works through bet-hedging/persistent strains

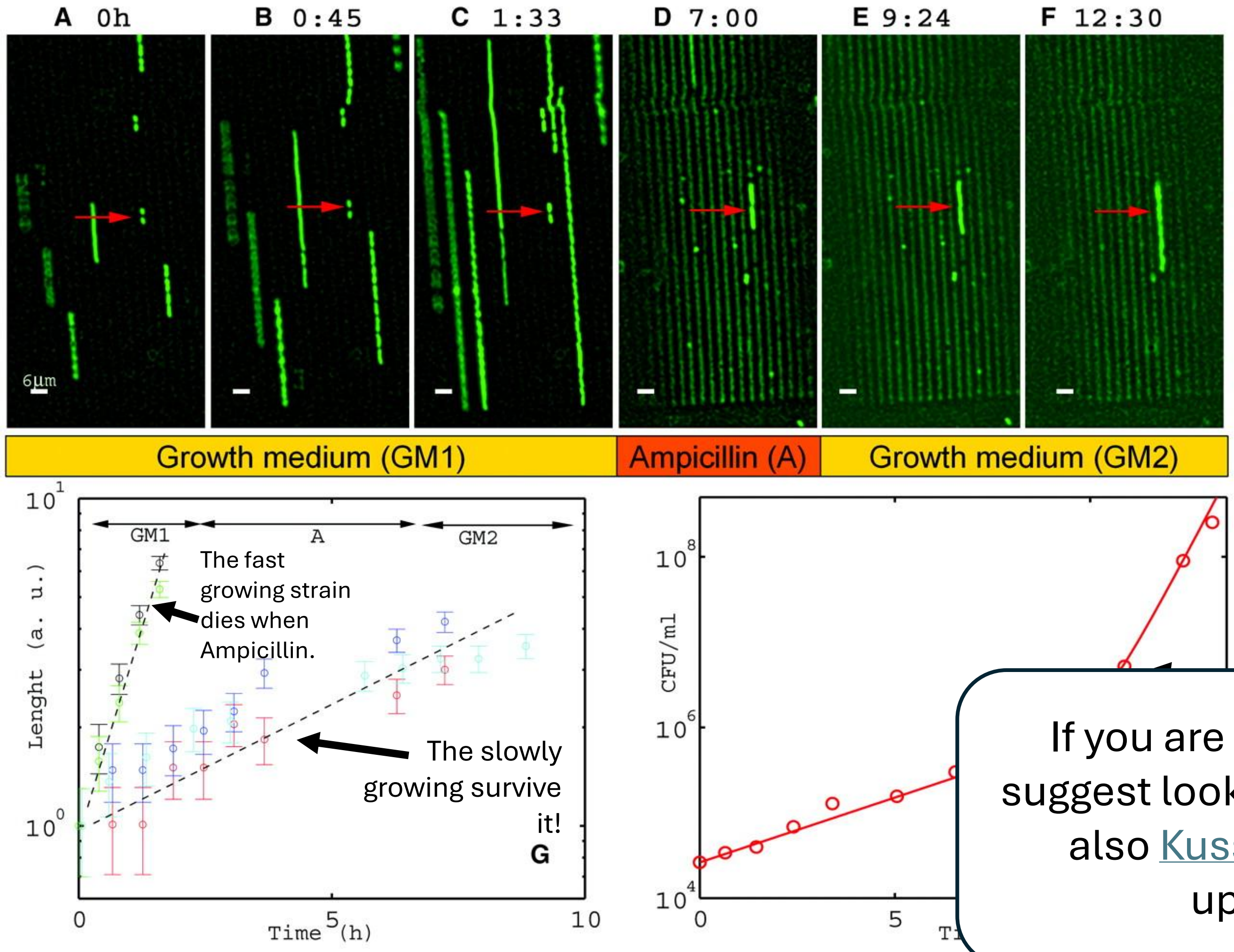


Type II switching (bet-hedging: slow growing resistant bacteria are constantly generated): *hipQ* mutant



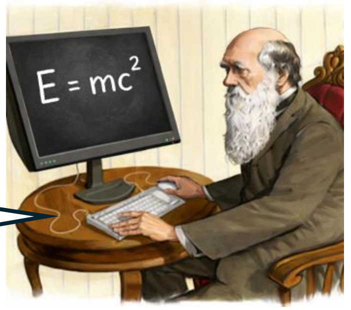
After exposure to Ampicillin the slowly growing strain speeds up growth again

Bacterial resistance to stress and antibiotic also works through bet-hedging/persistent strains

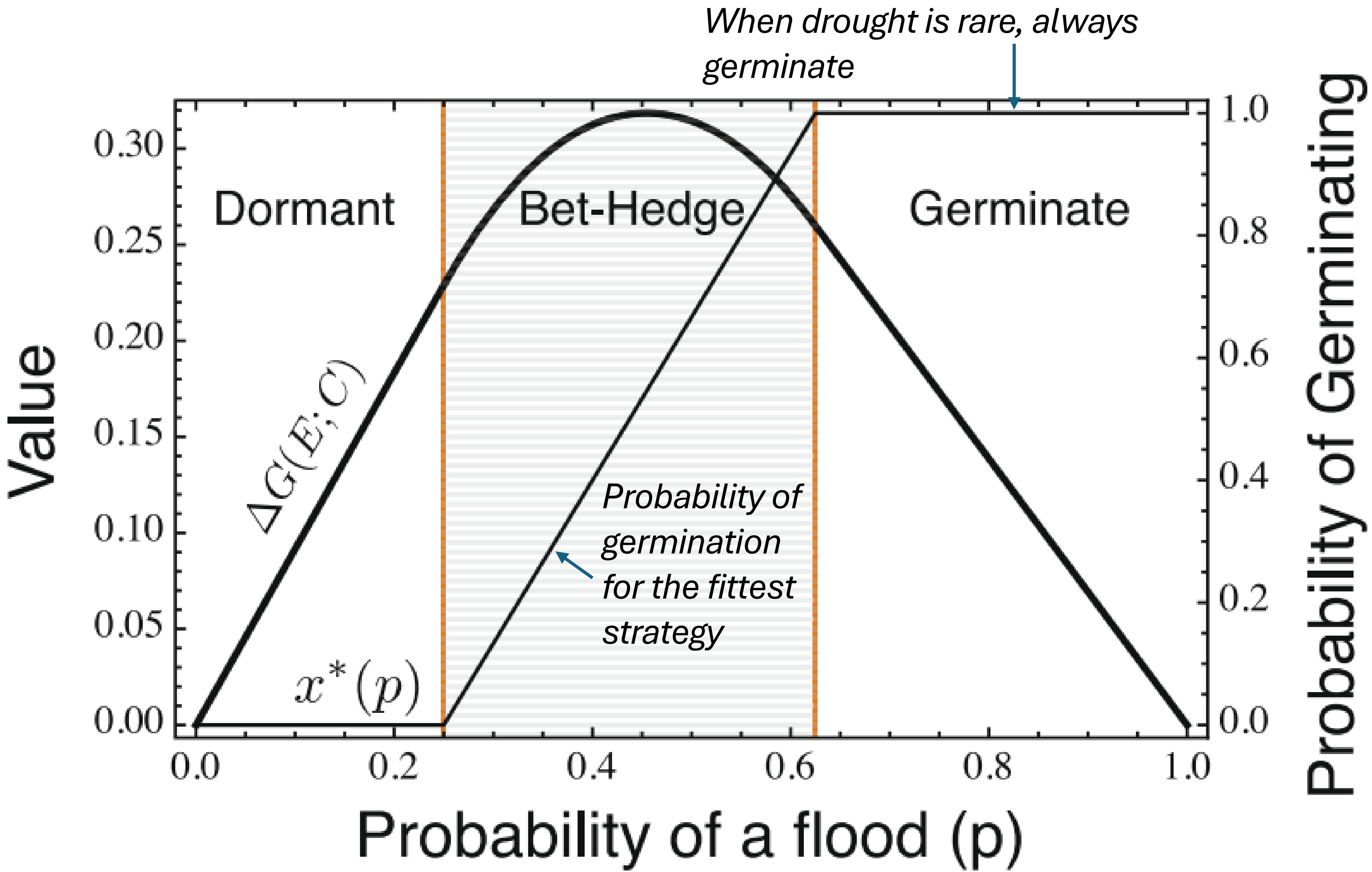


Type I persisters		Type II persisters	
Trigger; $n \rightleftarrows p_I$ (b)		$n \rightleftarrows p_{II}$ (a, b)	
$\begin{cases} \frac{dp_I}{dt} = -bp_I + \mu_p p_I \\ \frac{dn}{dt} = bp_I + \mu_n n \end{cases}$ Eq.(1)		$\begin{cases} \frac{dn}{dt} = -an + bp_{II} + \mu_n n \\ \frac{dp_{II}}{dt} = an - bp_{II} + \mu_p p_{II} \end{cases}$ Eq. (2)	
Estimated rates (units: hours^{-1})			
hipA7: $b=0.07\pm0.01$	*wt* Type I subpopulation: μ_p-b= -0.05±0.01*(23)*	*wt* Type II subpopulation: a=1.2±0.2 x10^{-6} b=0.1±0.05	*hipQ* a=1.0±0.2x10^{-3} $10^{-7}<b<10^{-4}$

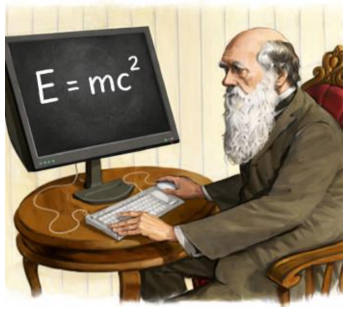
If you are curious about the model I suggest looking at the original paper and also Kussel et al.,2005, Genetics, uploaded on Moodle



When it is not a life or death situation, the probability of germinating is not exactly that of the wet-year



	Flood	Drought
Germinate	5	1
Dormant	2	2



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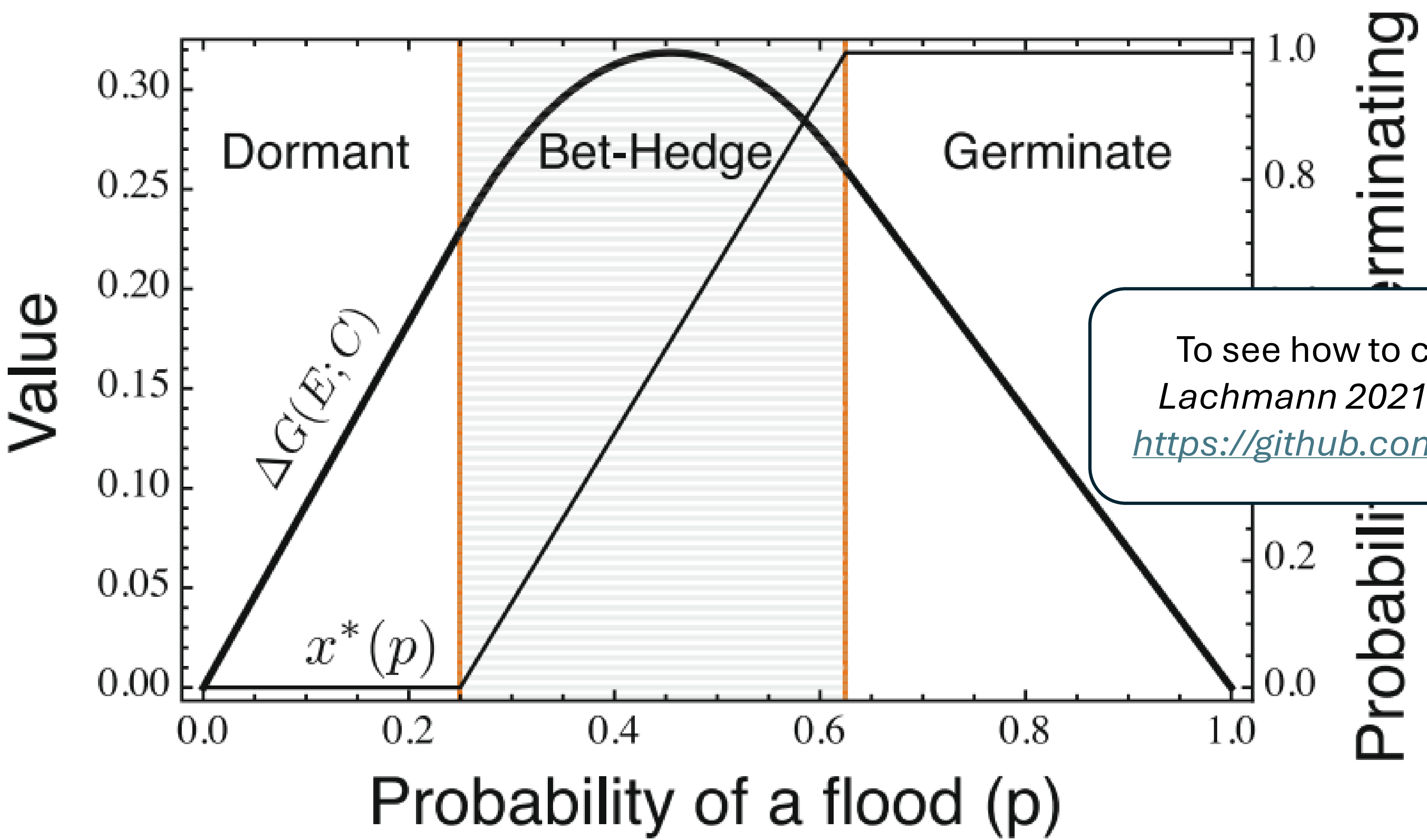

	Flood	Drought
Germinate	5	1
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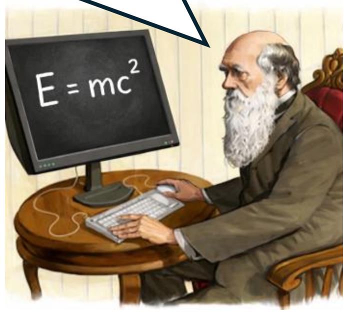
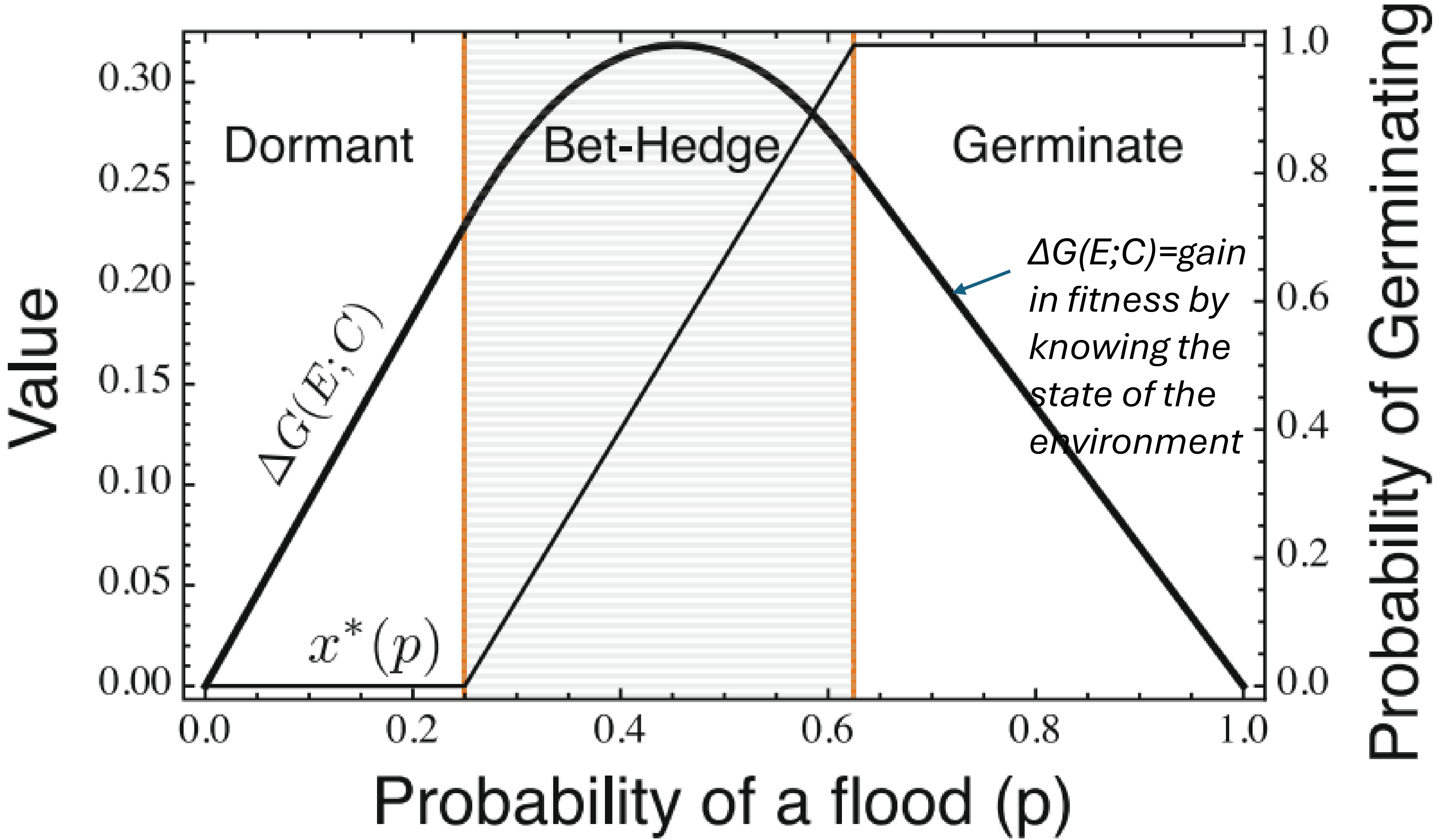
To see how to calculate it, read *Mafessoni & Lachmann 2021, JTB or its github for the code:* https://github.com/fabrimafe/fitness_value_cues



Plasticity (using an informative cue) gives a benefit in terms of fitness



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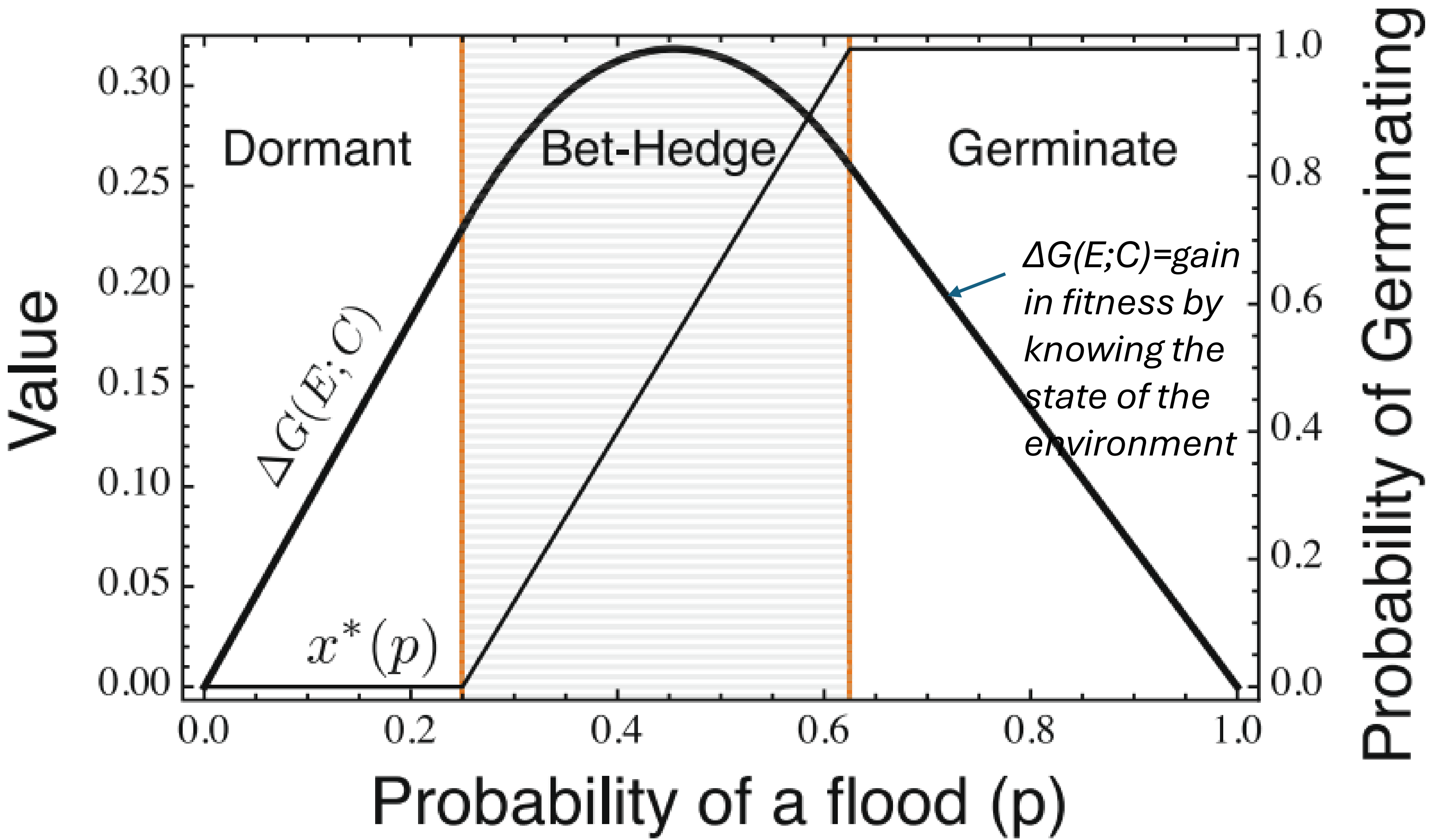

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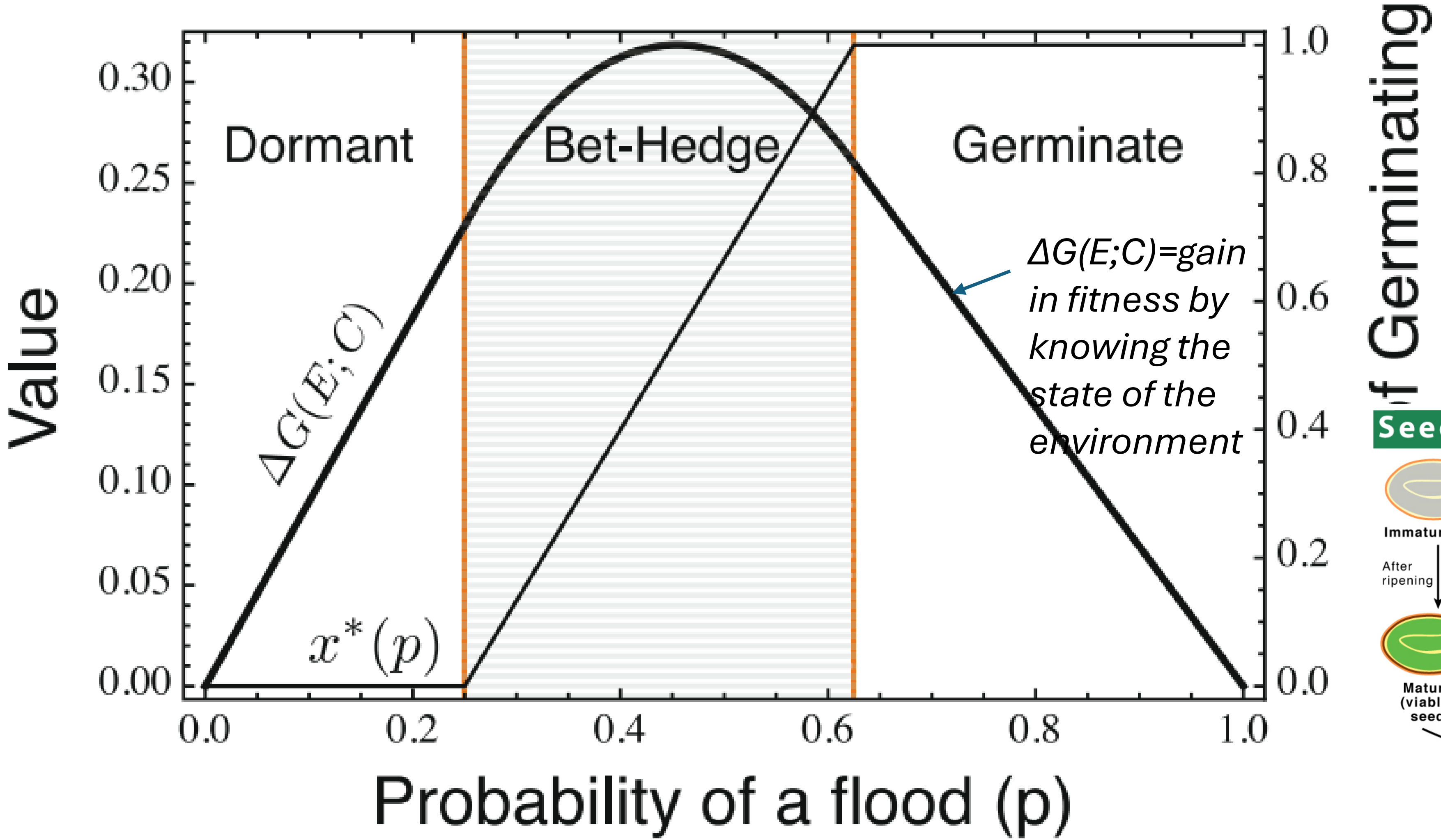
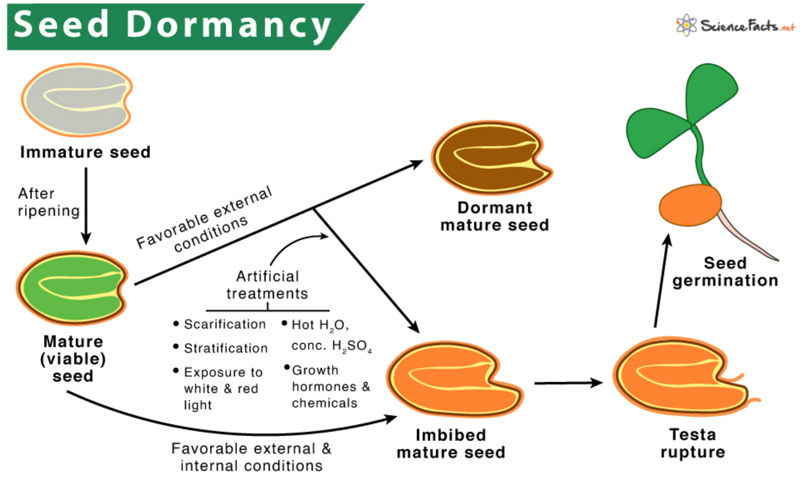


	Flood	Drought
Germinate	5	1
Dormant	2	2

This is how learning/plasticity evolves!



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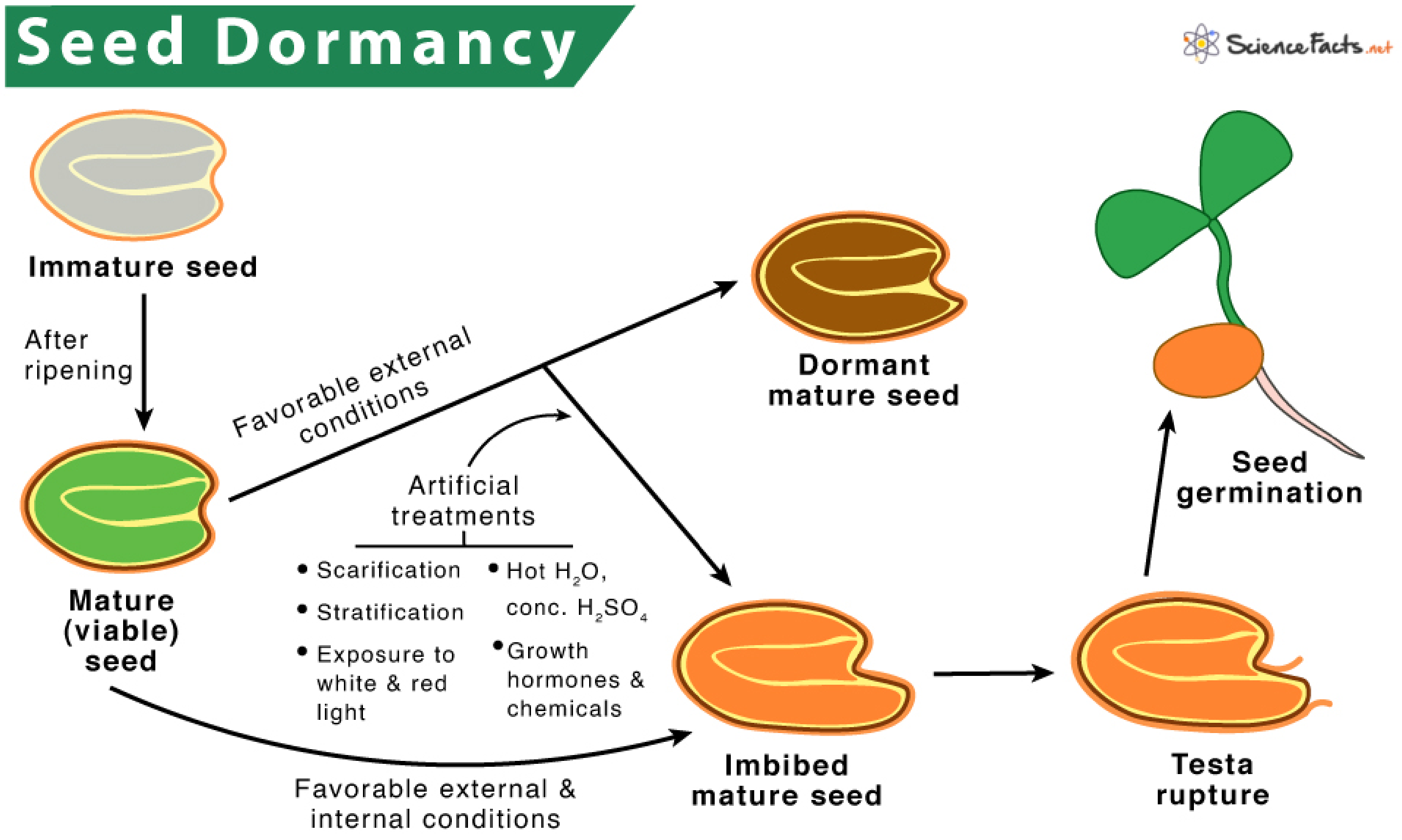

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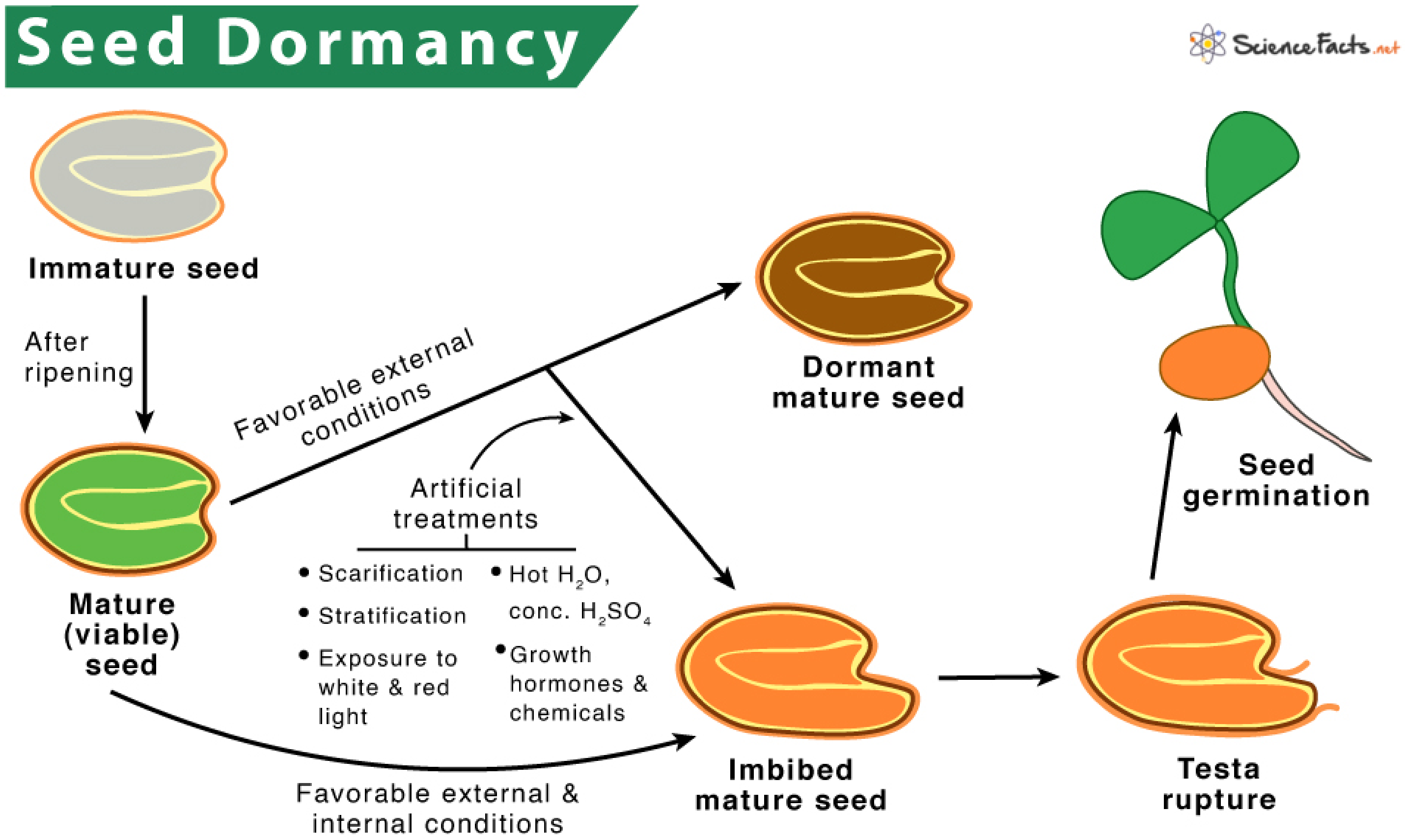
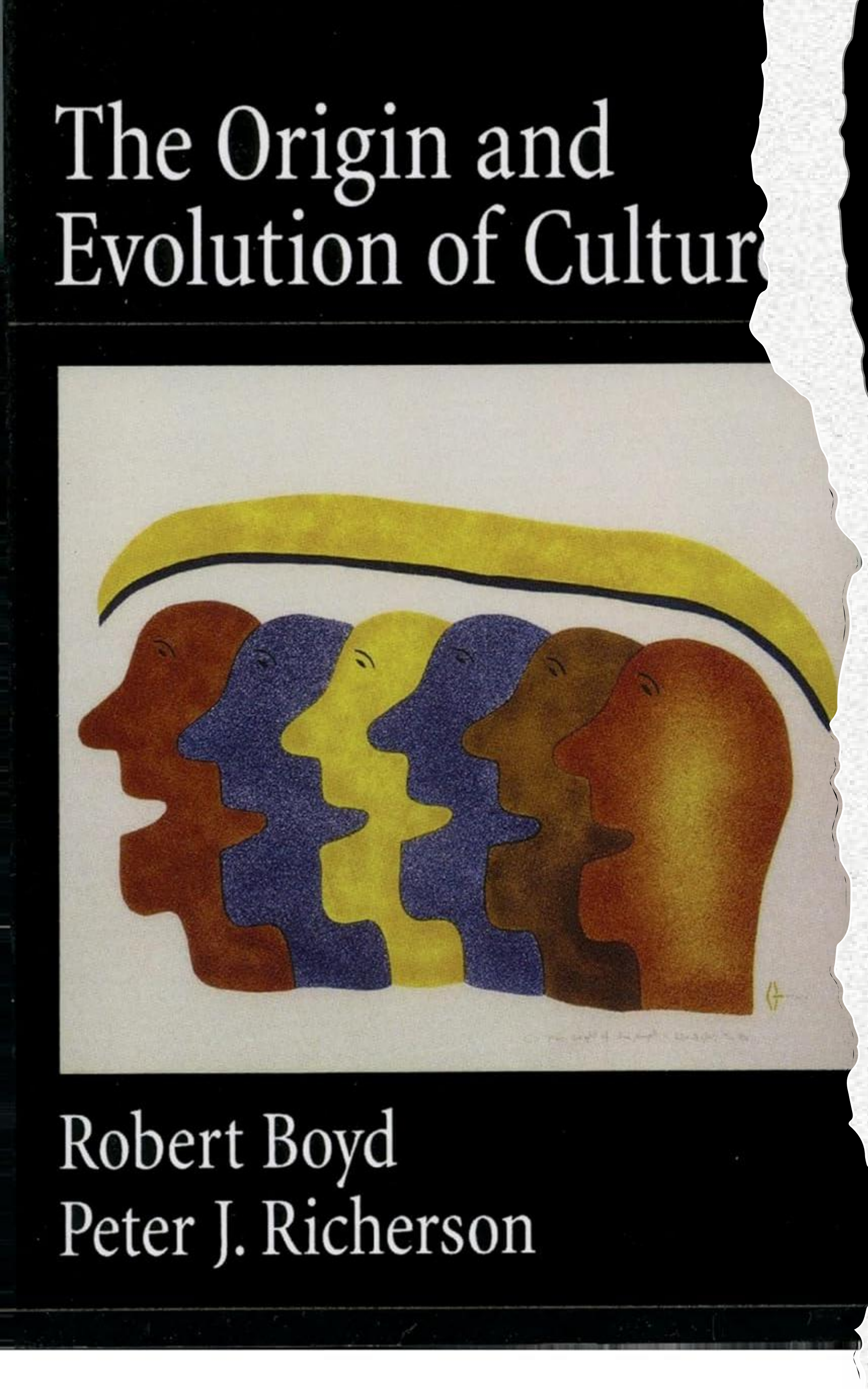


So why desert plants cannot just sense water?

What seeds can detect:
Soil moisture *now*
Temperature
Sometimes duration of hydration
What they cannot know:
Will it rain again next week?
Will the soil stay moist long enough to reproduce?
This is a **prediction problem**, not just a detection problem
It is a **"false start" problem:**
Scenario:
Rain falls → seeds detect water → germinate
Soil dries quickly
Seedlings die before reproducing



How does evolution shape this learning

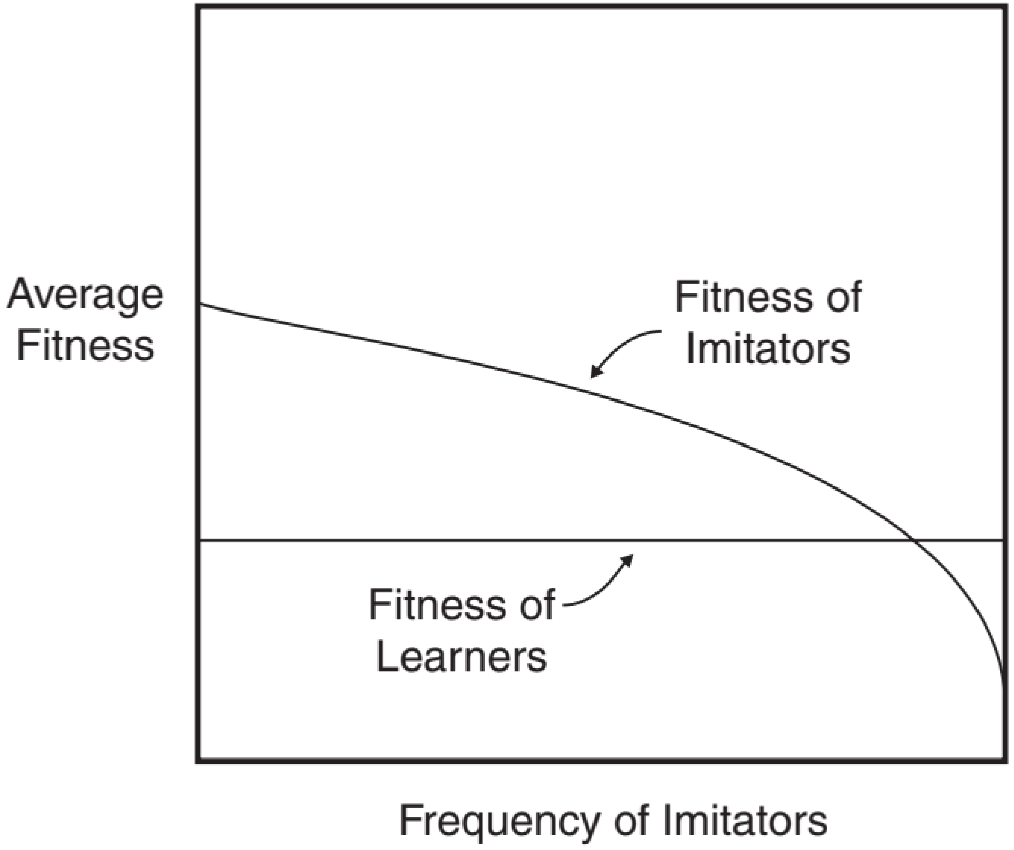
The evolution of social learning

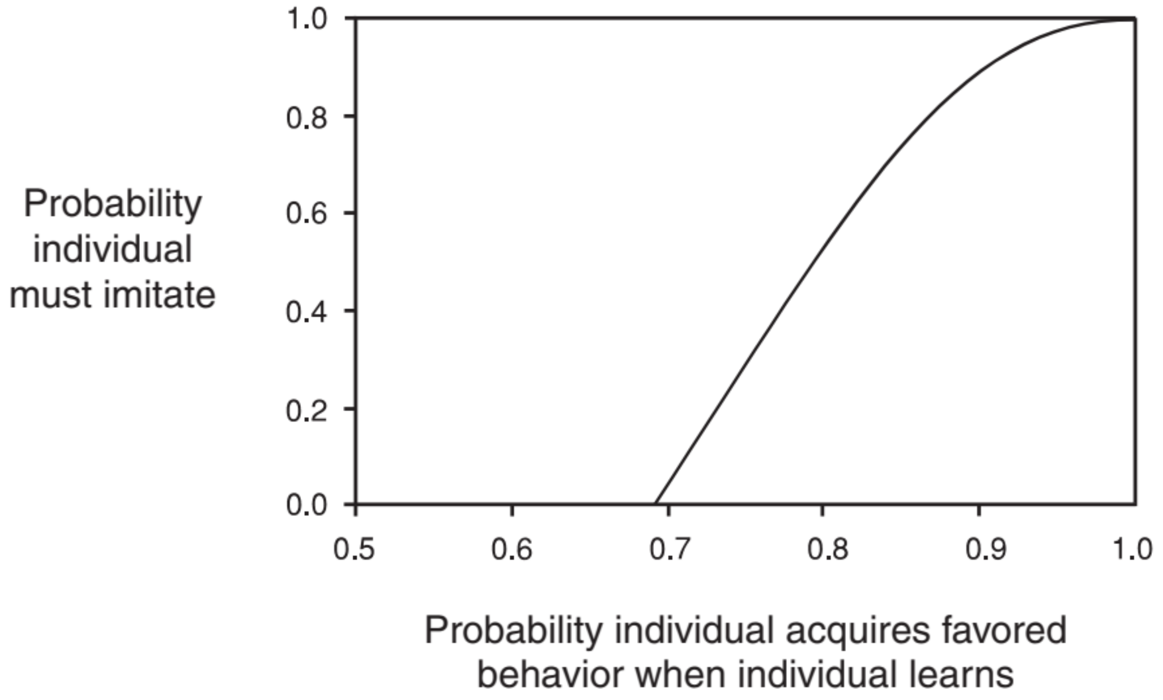
	Individual learning	Social learning
Individual learning	sB– c	sB-c
Social learning	sB	bB

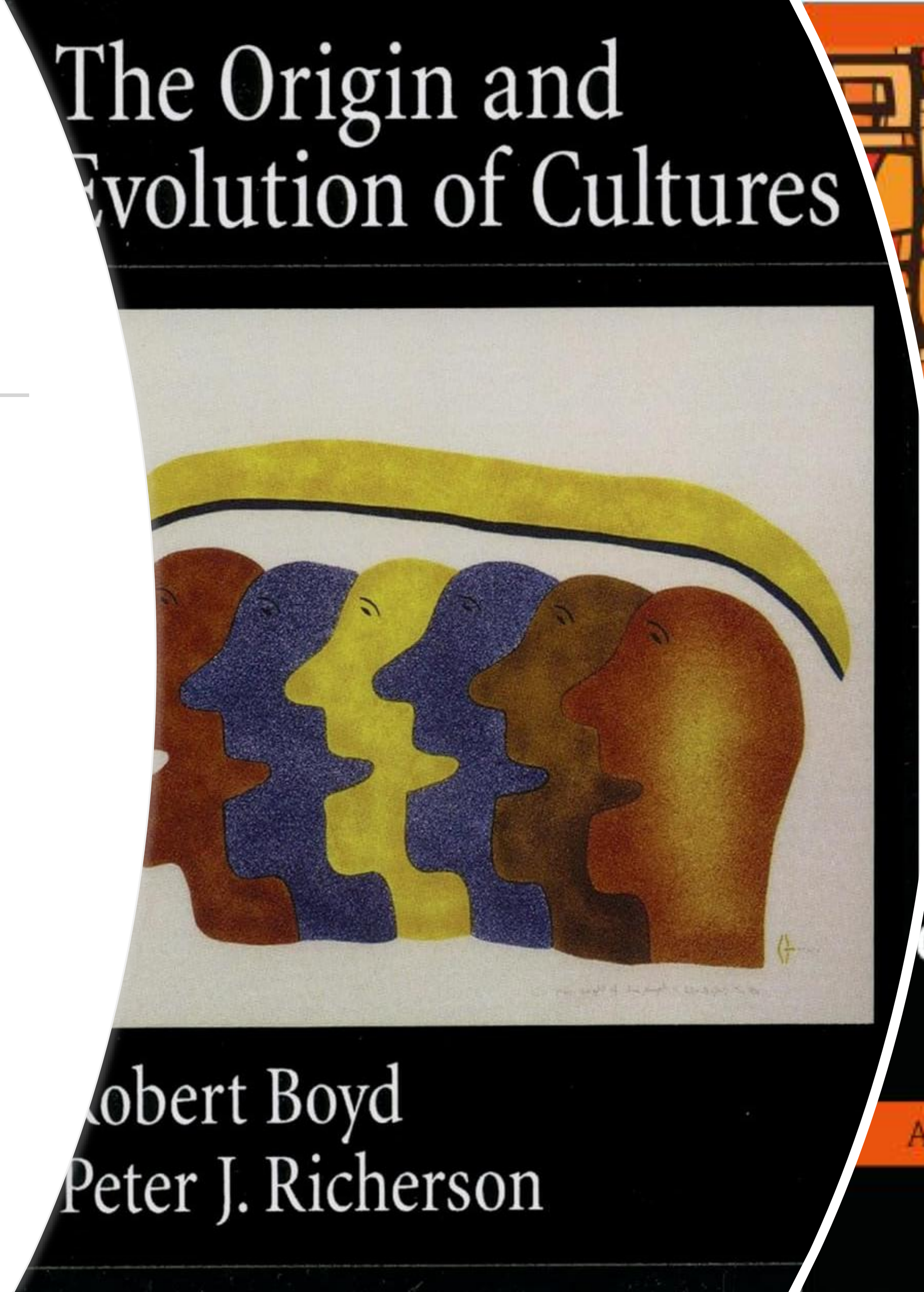
	Rain	Drought
Farming (or umbrella)	B	0
Herding (swimsuit)	0	B

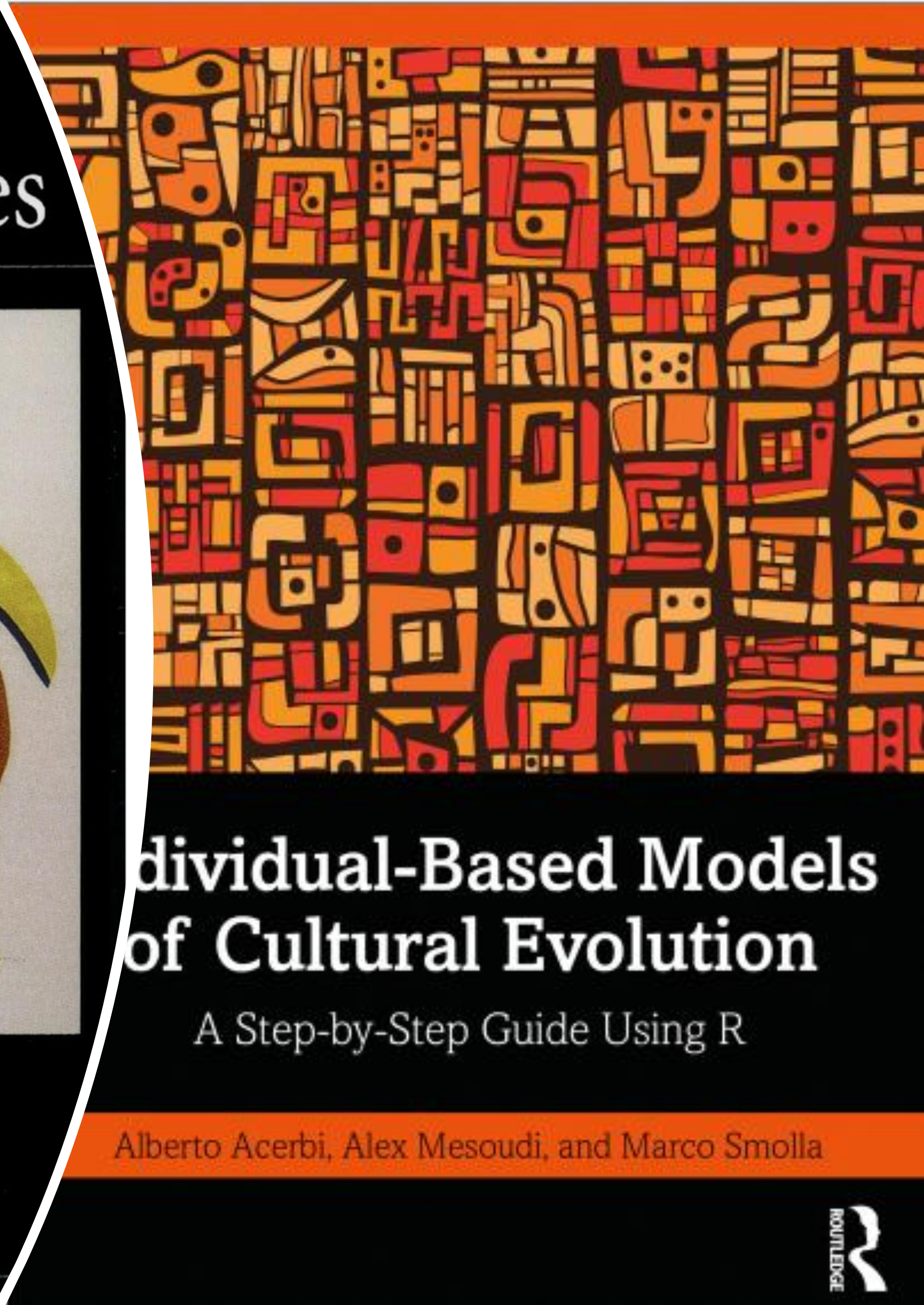
- s: accuracy of individual learning
- B: benefit of using the correct behavior
- c: cost of individual learning
- b: probability that the model is using the right behavior

Social learning evolves until too many imitators prevent innovation






The Origin and
Evolution of Cultures
Robert Boyd
Peter J. Richerson

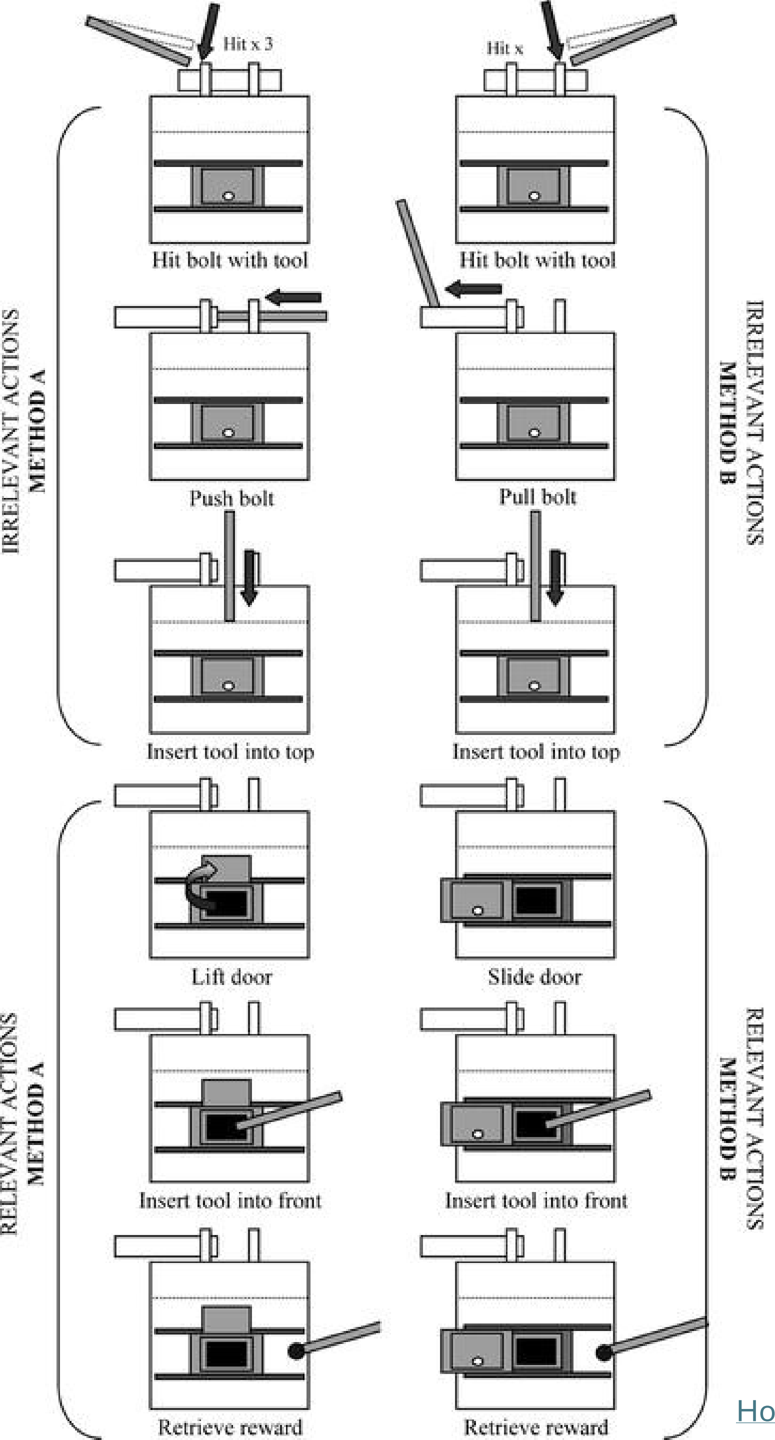

dividual-Based Models
of Cultural Evolution
A Step-by-Step Guide Using R
Alberto Acerbi, Alex Mesoudi, and Marco Smolla
ROUTLEDGE

Conformity bias

Overimitation

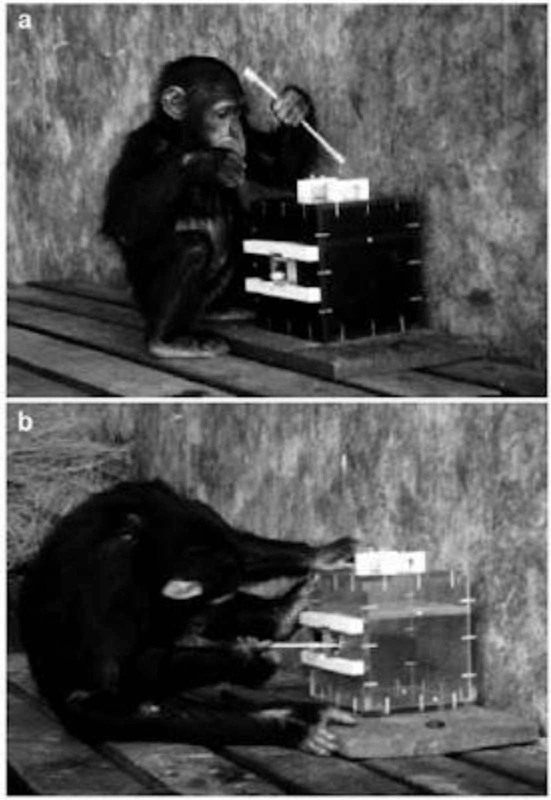
- "Humans don't just copy what works —
  they copy *how things are done*."

- More complex than just conformity – norms – but still a key component of our learning as children.



Children «monkey» others much more than other primates!

- "Humans don't just copy what works — they copy *how things are done*."
- Imitation and overimitations are more complex than just conformity – norms – but still a key component of our learning as children.
- Even chimpanzee do not truly imitate, even less overimitate



Horner & Whiten, 2005, Animal Cognition

Cultures in chimpanzees

A. Whiten[*], J. Goodall[†], W. C. McGrew[‡], T. Nishida[§],
V. Reynolds[||], Y. Sugiyama[¶], C. E. G. Tutin[#☆],
R. W. Wrangham[**] & C. Boesch[††]

- Dozens of cultural behaviors differ between chimpanzee communities across Africa
- Evidence for culture in many other non-human primates (e.g. Capuchin monkeys for nut-cracking) and species, among which corvids, cetaceans, and many others
- No evidence for cumulative cultures (culture that stratifies through successive modifications) in non-human animals however – possibly due to the lack of faithful imitation/social transmission and cognitive biases like conformity bias

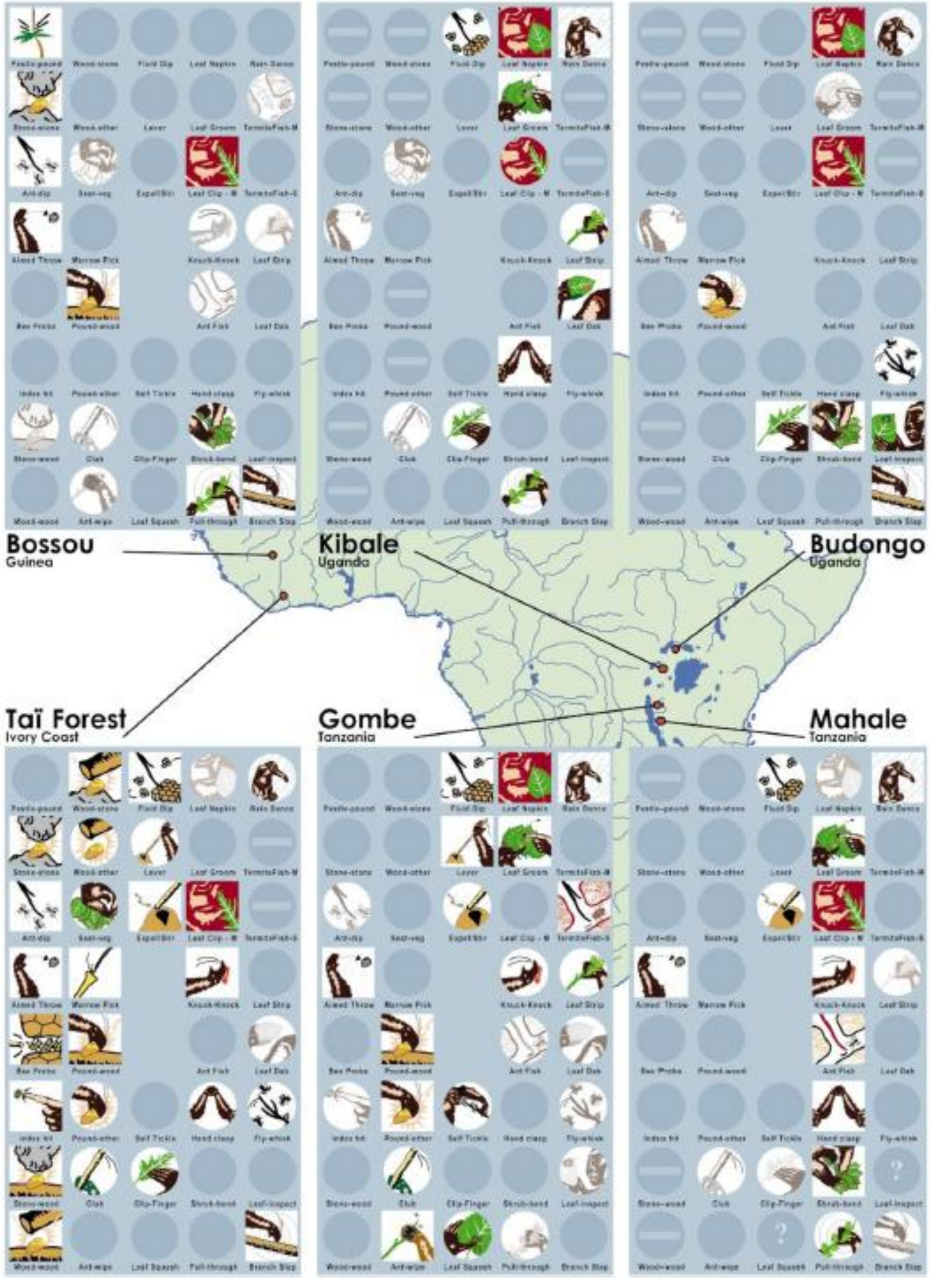


Figure 1 Distribution of behaviour patterns from band D in Table 1 across six African study sites. Behaviours are arranged in the 5 × 8 arrays to cluster those behaviours customary or habitual at each site, with clusters for westerly sites on the left of the array and clusters for easterly sites on the right. The secondary Mahale site (K) is omitted. Colour icons, customary; circular icons, habitual; monochrome icons, present; clear, absent; horizontal bar, absent with ecological explanation; question mark, answer uncertain.

Conclusion

- Environmental change can be abrupt, leaving little space for natural selection and a lot to stochastic effects
- In presence of environmental uncertainty maximizing short-term fitness is not necessarily the best strategy, while it is often convenient to hedge one’s bets
- Environmental uncertainty promotes the evolution of learning and plasticity
- Evolution shapes the types of learning/plasticity which will evolve, shaping cognition and culture through learning mechanisms and cognitive biases, such as conformity bias and overimitation
- Culture is not uniquely human, while evidence of cumulative culture is scarce in other species