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GUEST LECTURE
November 28, 2016

Taking History Seriously: causality and patterns in evolutionary systems

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1. Experimental sciences VS historical sciences?

HISTORICAL SCIENCES:
No re-testing
No counter-factuals
No clear repetitions
Different epistemic situations, etc.

↓

A «secundary status» with respect to EXPERIMENTAL SCIENCES?
(Earth sciences, palaeontology, evol. biology, astrophysics?)

"Hypotheses about the remote past can never be tested by experiment, and so they are unscientific. No science can ever be historical"
(Henry Gee, 1999, p. 5)

(cladistics – nomothetic palaeontology)

The **division between nomothetic and historical sciences** does not mean that each science is exclusively one or the other. The particle physicist might find that the collisions of interest often occur on the surface of the sun; if so, a detailed study of that particular object might help to infer the general law. Symmetrically, the astronomer interested in obtaining an accurate description of the star might use various laws to help make the inference. … The same division exists within evolutionary biology. … Although inferring laws and reconstructing history are distinct scientific goals, they often are fruitfully pursued together. Theoreticians hope their models are not vacuous; they want them to apply to the real world of living organisms. Likewise, naturalists who describe the present and past of particular species often do so with an eye to providing data that have a wider theoretical significance. **Nomothetic and historical disciplines in evolutionary biology have much to learn from each other**.

Elliott Sober (2000) *Philosophy of Biology*, pp. 14-15

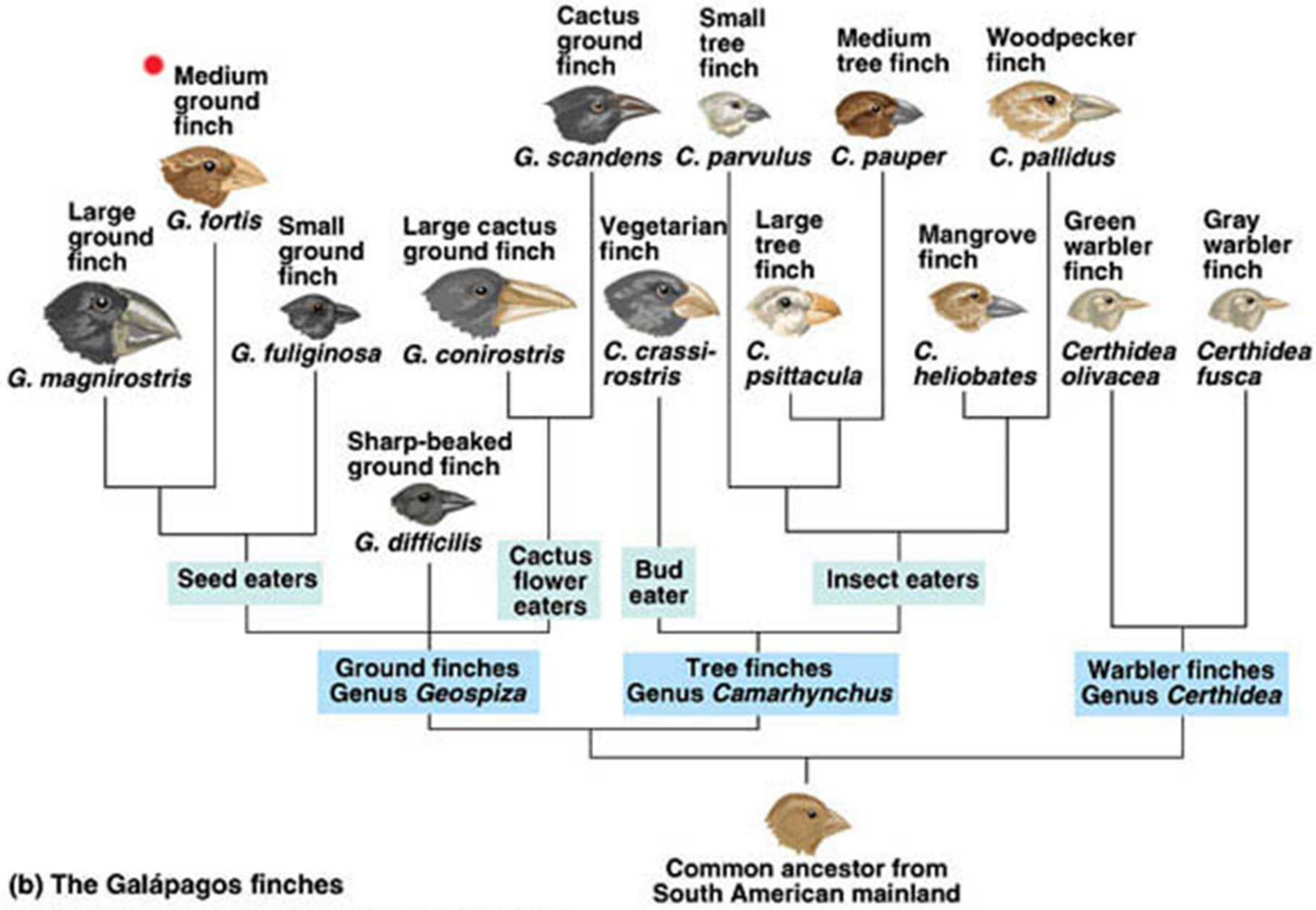
It is quite impossible to find the exclusive cause of a particular phenomenon in biology. Biology is the science of multiple causes, plus the probabilistic feature of the chain of events.

(Ernst Mayr, 1997)

PROXIMATE CAUSES
(immediate physiological and mechanical factors; how eye works)

+

REMOTE CAUSES
(evolutionary forces acting on traits; how eye evolved)



(b) The Galápagos finches

Which causes for this adaptive radiation?

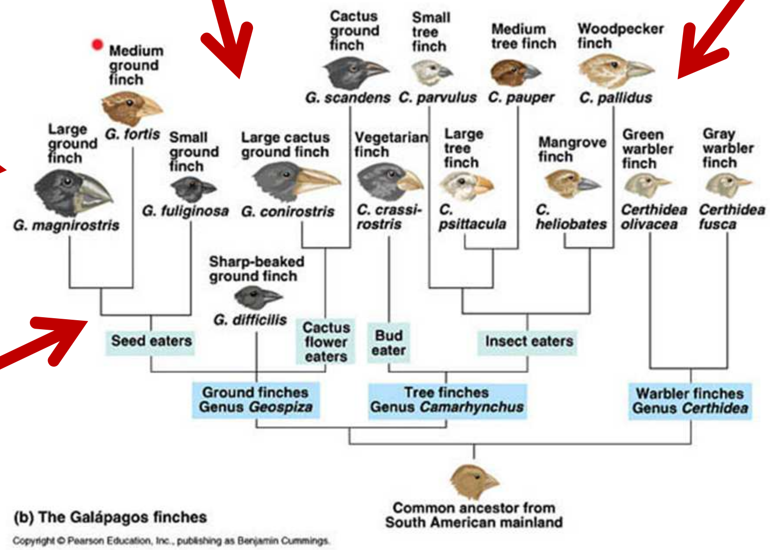
Natural and sexual selection

Random genetic drift

Cultural as well as genetic evolution

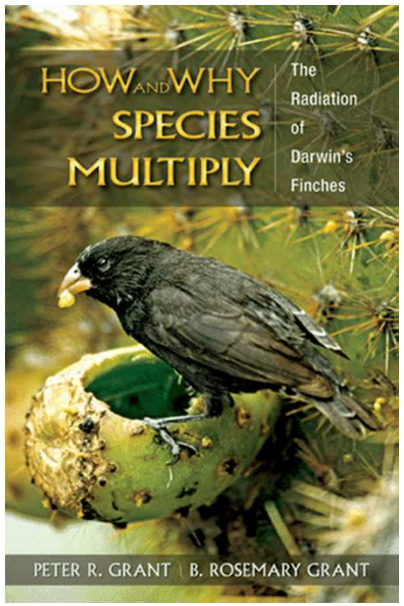
Hybridization

Fluctuations in climatic conditions



(b) The Galápagos finches

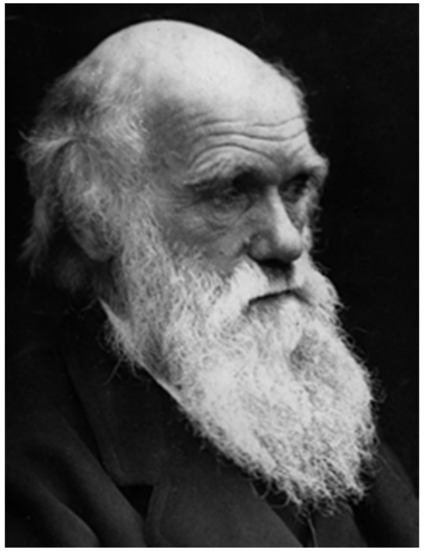
«In this book we attempt to explain the evolutionary diversification of Darwin's finches in terms of geography, behavior, ecology, and genetics. The explanation involves **natural and sexual selection, random genetic drift, exchange of genes through hybridization (introgression), and cultural as well as genetic evolution**. Linking all these factors together is the **frequent and strong fluctuation in climatic conditions**» (R. and P. Grant, 2008, p. 11)



Obs. 1: Exponential growth of populations

Obs. 2: The balance of populations

Obs. 3: Limited resources



Ded. 1: Struggle for existence

Obs. 4: Individual diversity

Obs. 5: Heredity of a part of the individual variation

Obs. 6: Variation is not externally directed

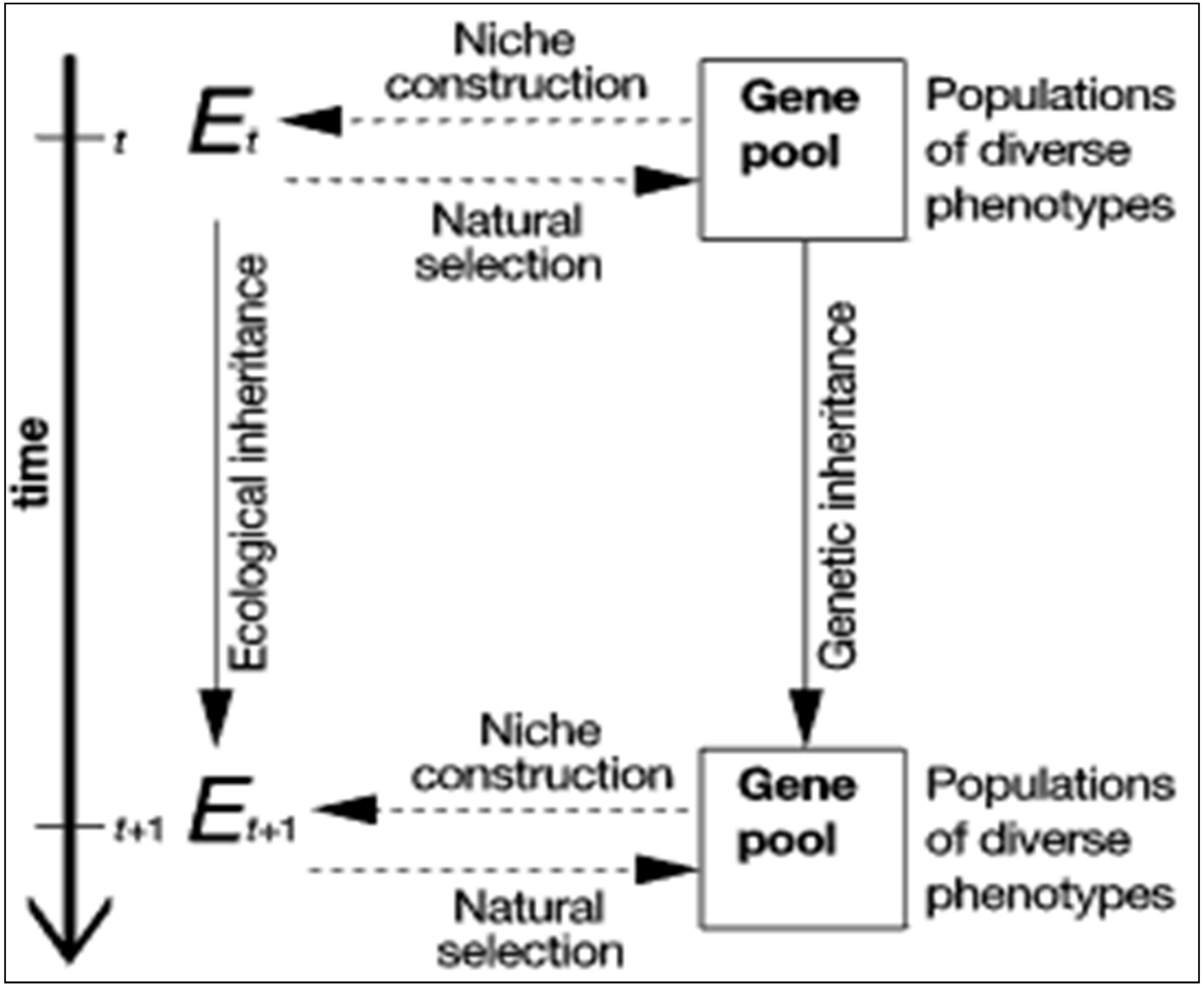
Ded. 2: Differential survival

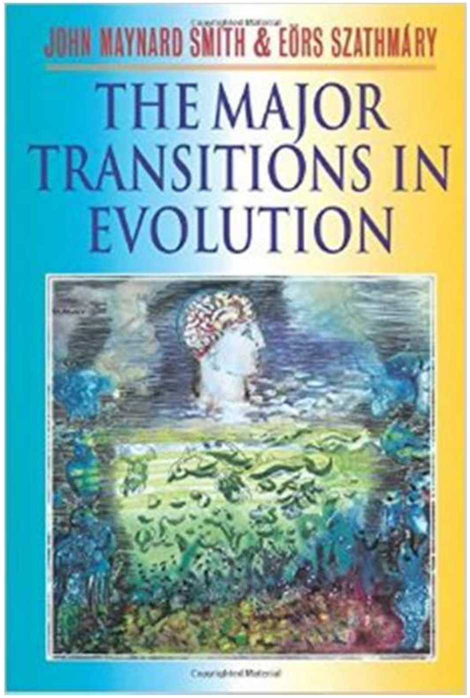
Ded. 3: Differential reproductive success, over generations: change within populations.

Ded. 4: (Principle of divergence) Descent with Modifications

- Natural selection IS NOT a «UNIVERSAL LAW» like those we know in physics
- Natural selection makes some effects more PROBABLE than others

RECIPROCAL CAUSATION
(Niche construction)





Replicating molecules →	Populations of molecules
Independent replicators →	Chromosomes
RNA →	DNA
Prokaryotes →	Eukaryotes
Asexual clones →	Sexual populations
Protists →	Animals, plants, fungi
Solitary individuals →	Colonies
Primate societies →	Human societies, **Language**

The «laws» of evolution themselves evolve…
(contingency thesis)

“We may define a cause to be **an object followed by another, and where all the objects, similar to the first, are followed by objects similar to the second**. Or, in other words, where, **if the first object had not been, the second never had existed**.”

Regulatory definition of causality

Counterfactual definition of causality

(DAVID HUME, 1748)

Counterfactual theory of causation - David Lewis 1973: “non-actual possible worlds are real concrete entities”

CAUSE: “We think of a cause as something that makes a difference, and the difference it makes must be a difference from what would have happened without it. Had it been absent, its effects — some of them, at least, and usually all — would have been absent as well.”

COUNTERFACTUAL RESISTANCE

1. MAXIMUM – Deterministic process (no counterfactual possible; timeless and universal laws resulting in predictions)

2. MINIMUM – Random process (every counterfactual will have same likelihood)

3. MODULATION OF PROBABILITY – Evolutionary contingency (counterfactual probability depending on interplay between patterns and historical events)

EVOLUTIONARY CONTINGENCY

1) CONTINGENCY DOES NOT MEAN «PLAIN CHANCE»: IT IS AN **INTERPLAY BETWEEN REGULARITIES (PATTERNS) AND RANDOM EVENTS**.

2) CONTINGENCY IS A **MODULATION OF PROBABILITY** (DEPENDING ON THE RELATIVE POWER OF PATTERNS CASE BY CASE).

3) CONTINGENCY IS THE **CAUSAL POWER OF SINGLE EVENTS TO MODIFY HISTORICAL PATHS**: IT DEPENDS ON MULTIPLE INTERACTING CAUSES.

Sliding doors…

Is it possible to deal with contingency «scientifically»?

2. Singularities and patterns: the case of mass-extinctions

INSIGHTS

EVOLUTIONARY BIOLOGY

Leveling up

Advocates aim to stimulate renewed interest in a hierarchical theory of evolution

By **Bengt Autzen**

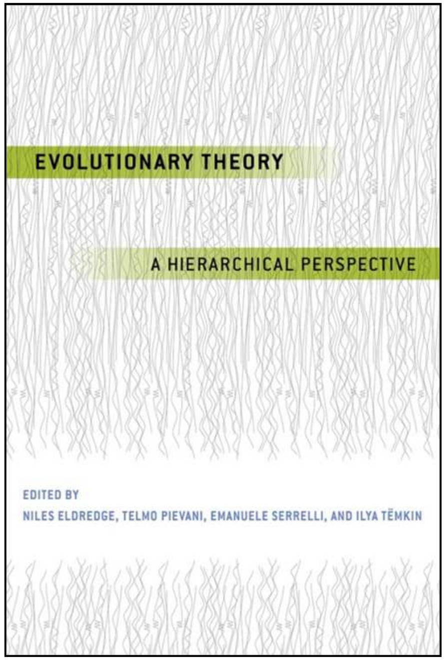
The second part of the book is dedicated to the dynamic relationships between entities at different levels of biological hierarchies. The essay contributed by evolutionary ecologist Mihaela Pavličev and collaborators—which develops an abstract theory of the behavior of emergent systems by examining structural similarities between biological systems at the molecular level and in human cultural evolution—was particularly illuminating.

The third and final part of the book turns to the notion of macroevolution,

Evolutionary Theory
A Hierarchical Perspective
Niles Eldredge, Telmo Pievani, Emanuele Serrelli, Ilya Tëmkin, Eds.
University of Chicago Press, 2016. 393 pp.

this structural feature is relevant for understanding evolution. Both interpretations are at play in the volume, but the distinction is not always clear.

30 SEPTEMBER 2016 • VOL 353 ISSUE 6307 **1505**



Levels in genomics

Systems biology

Multilevel selection

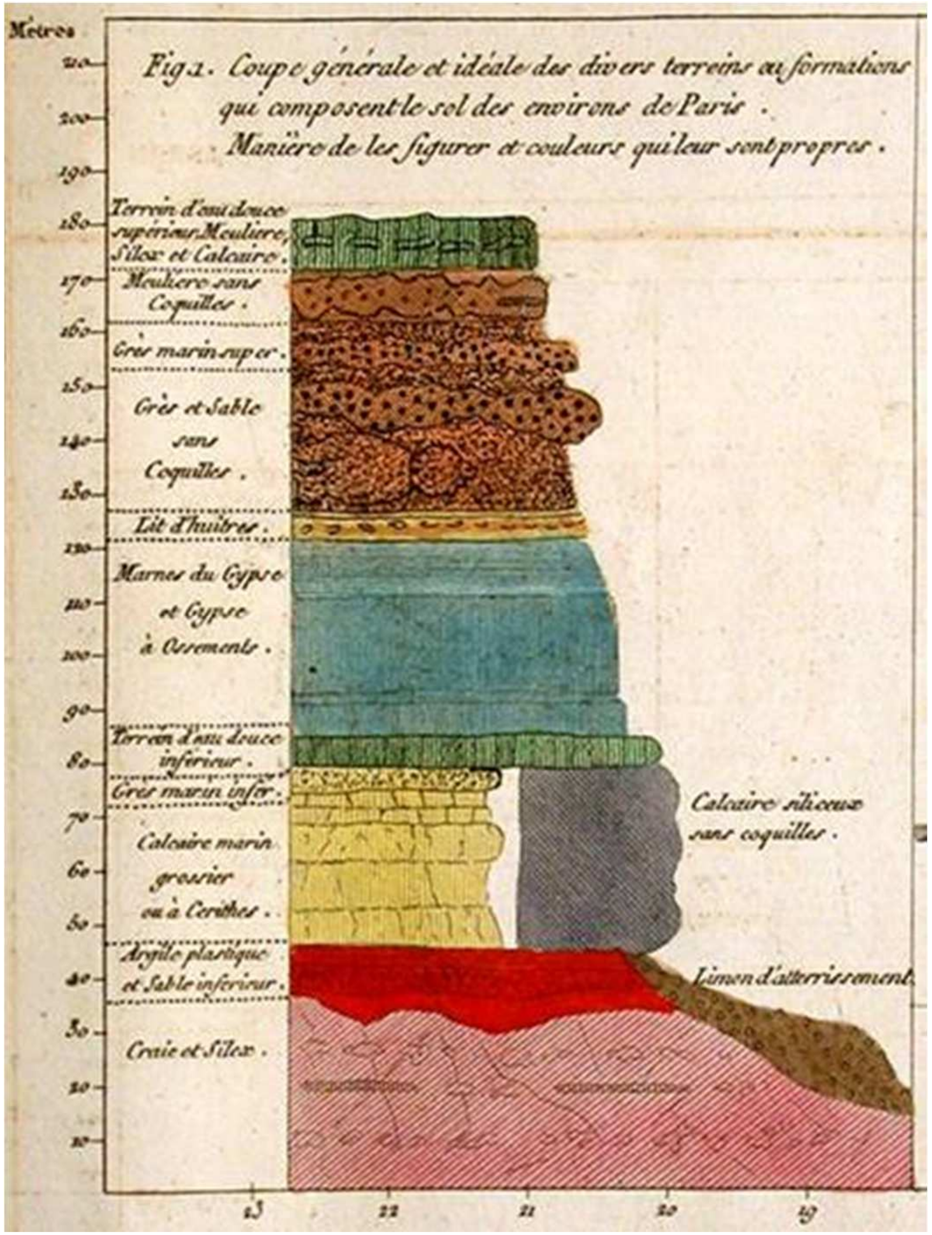
Tempo and mode of speciation

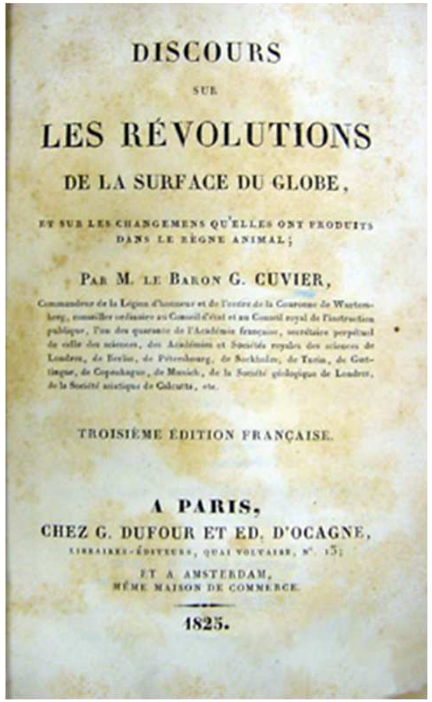
Macroevolutionary patterns

Mass-Extinctions

A neglected observation

Georges Cuvier (1769-1832)





DISCOURS
SUR
LES RÉVOLUTIONS
DE LA SURFACE DU GLOBE,
ET SUR LES CHANGEMENS QU'ELLES ONT PRODUITS
DANS LE RÈGNE ANIMAL;

PAR M. LE BARON G. CUVIER,

TROISIÈME ÉDITION FRANÇAISE.

A PARIS,
CHEZ G. DUFOUR ET ED. D'OCAGNE,

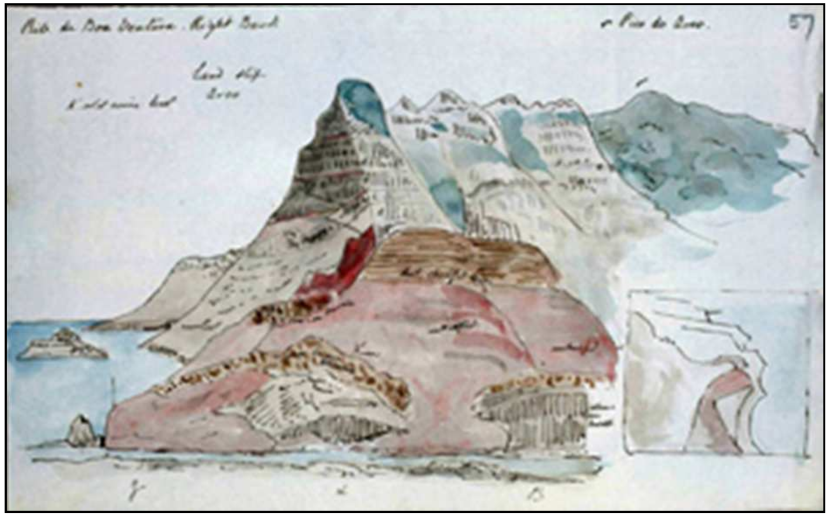
ET A AMSTERDAM,
MÊME MAISON DE COMMERCE.

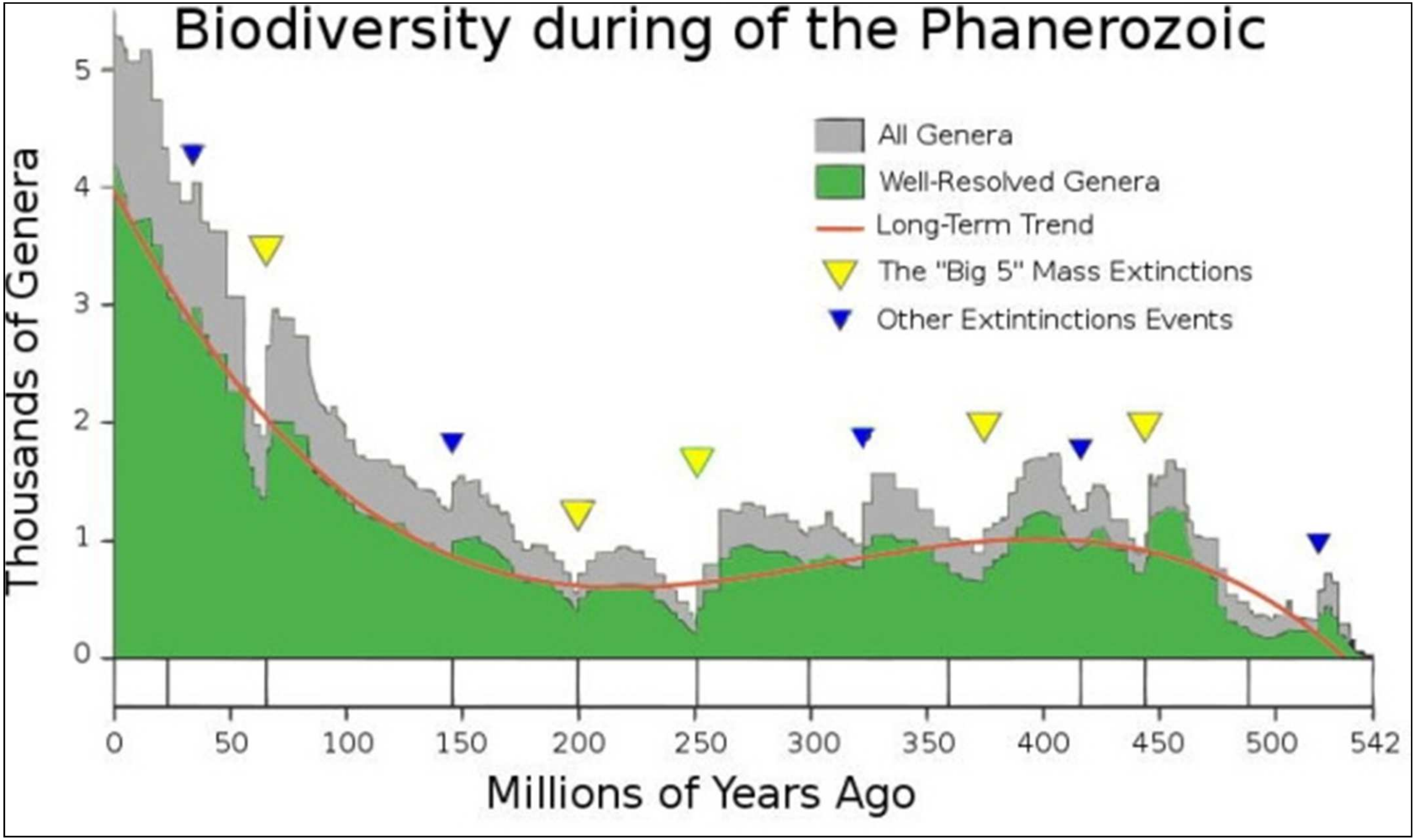
1825.

The refusal of catastrophism

"Never was there a doctrine more calculated to foster indolence, and to blunt the keen edge of curiosity, than this assumption of the discordance between the former and the existing causes of change... The student was taught to despond from the first. Geology, it was affirmed, could never arise to the rank of an exact science... [With catastrophism] we see the ancient spirit of speculation revived, and a desire manifestly shown to cut, rather than patiently untie, the Gordian Knot".

(Lyell, PoG, ed. 1854, p. 196)





(O. Nielsen, 2009)

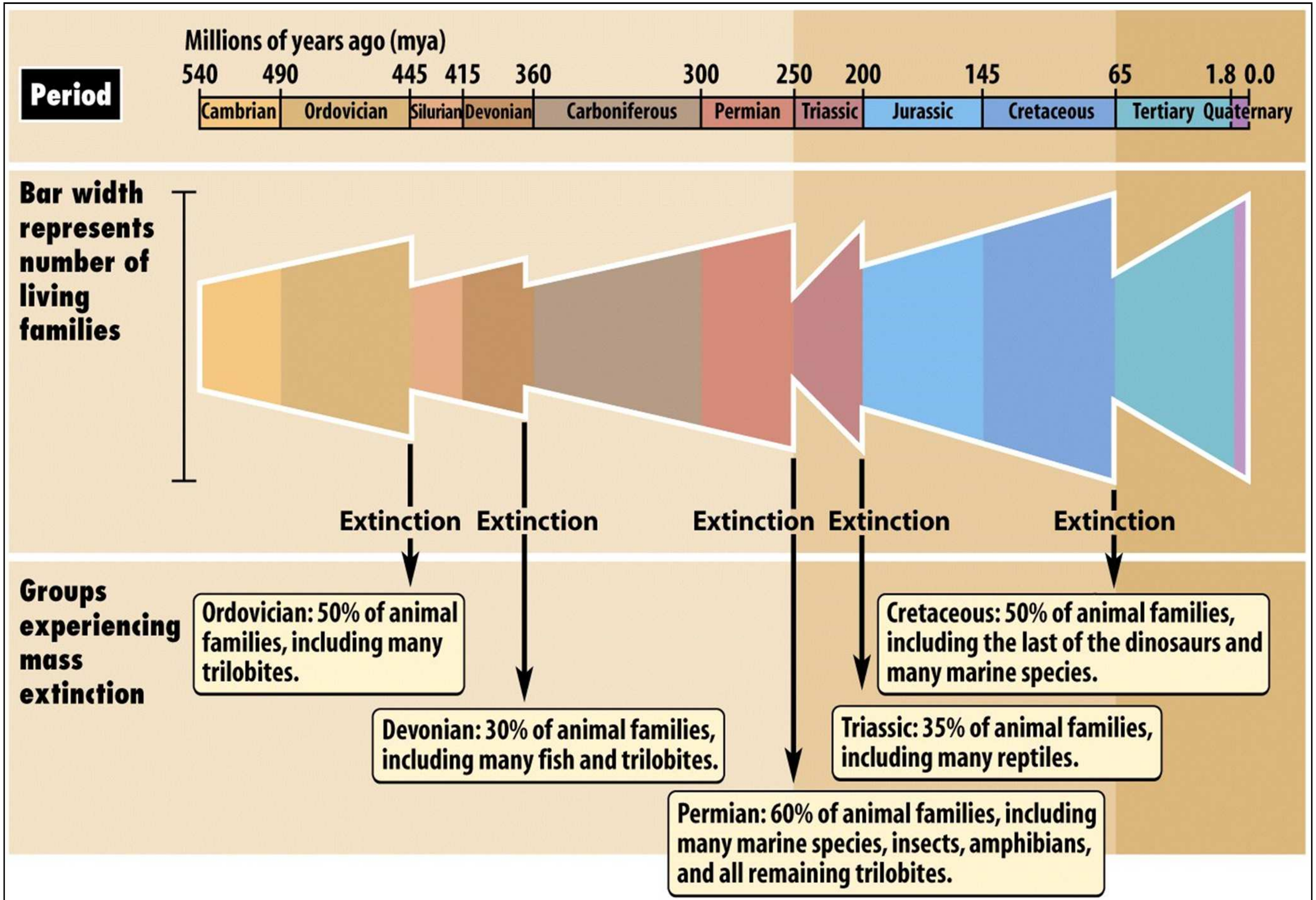
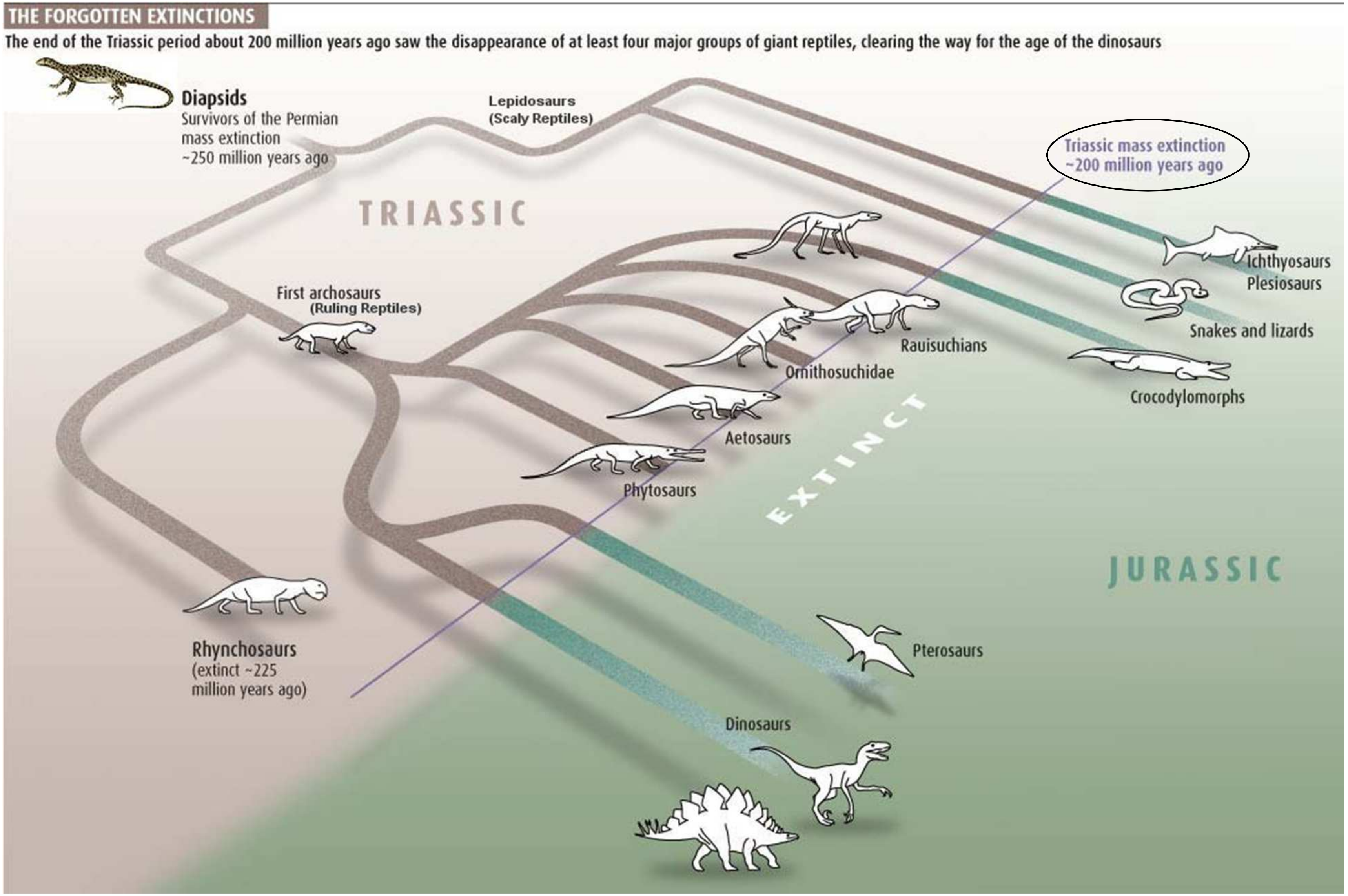
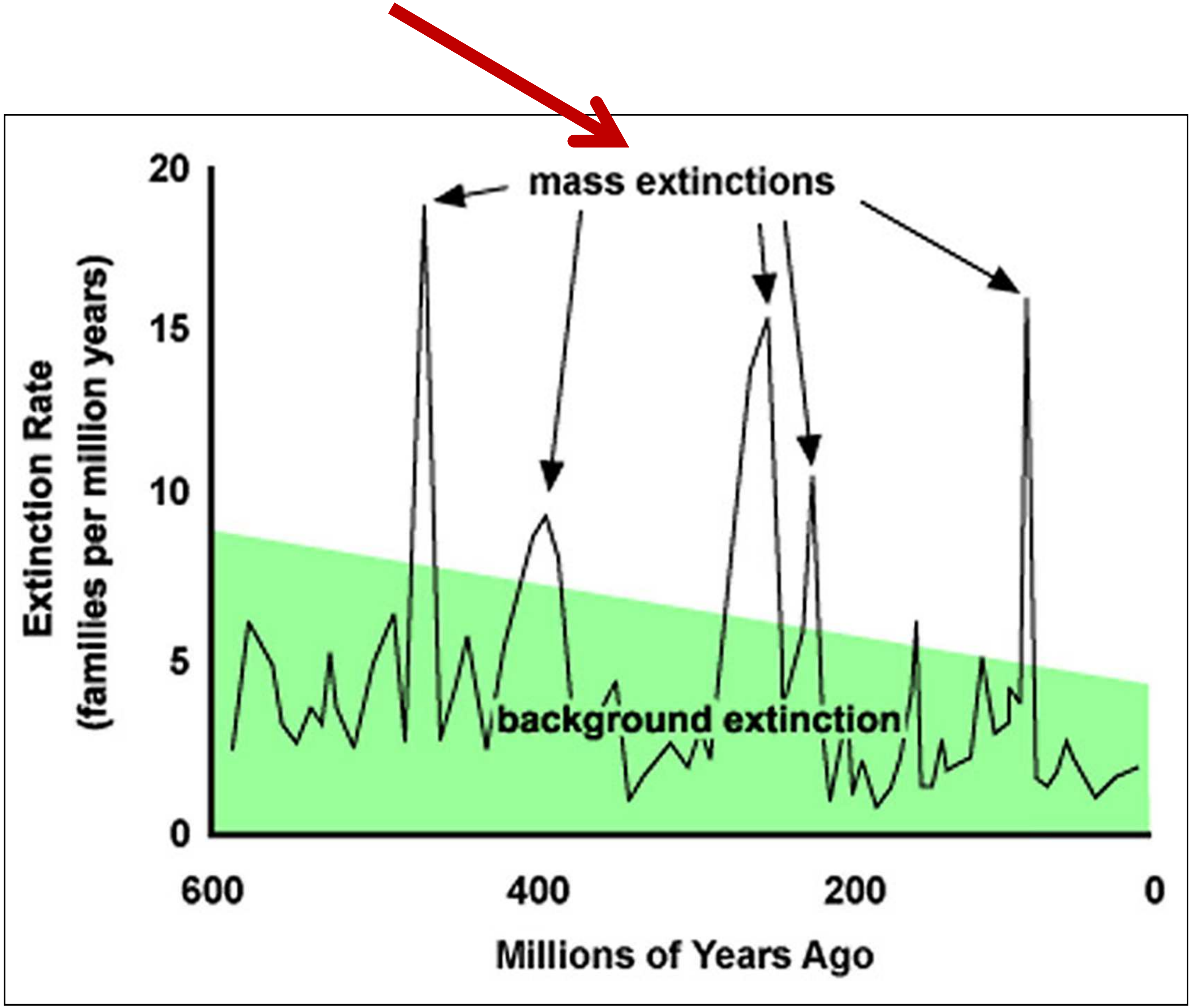


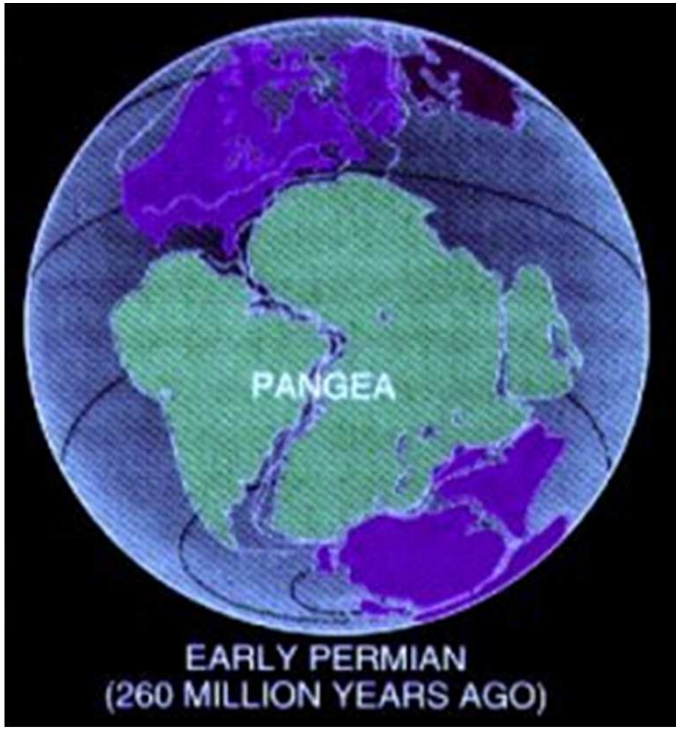
Figure 19-8 Discover Biology 3/e



Lucky (and unpredictable) survivors

Frequency, high magnitude, «rapidity», low selectivity, no intensification of ordinary causes





Large scale
contingent causes

But… THE "PERFECT STORM" MODEL FOR MASS-EXTINCTIONS

- Arens, N.C. e I.D. West, 2008, Press-pulse: A general theory of mass extinctions?, in «Paleobiology», 34, pp. 456-471.
- Brook, B.W., N.S. Sodhi e C.J.A. Bradshaw, 2008, *Synergies among extinction drivers under global change*, in "Trends in Ecology & Evolution", 23, pp. 453-460.

1 – Accelerated climate changes.

2 – Alterations of atmosphere composition.

3 – Ecological stresses with abnormal intensity.

1-3 (positive feedbacks)

= "loss of more than three-quarters of species in a geological short interval".

Plurality of causes for the same pattern

A somehow familiar pattern?

REVIEW

doi:10.1038/nature09678

Has the Earth's sixth mass extinction already arrived?

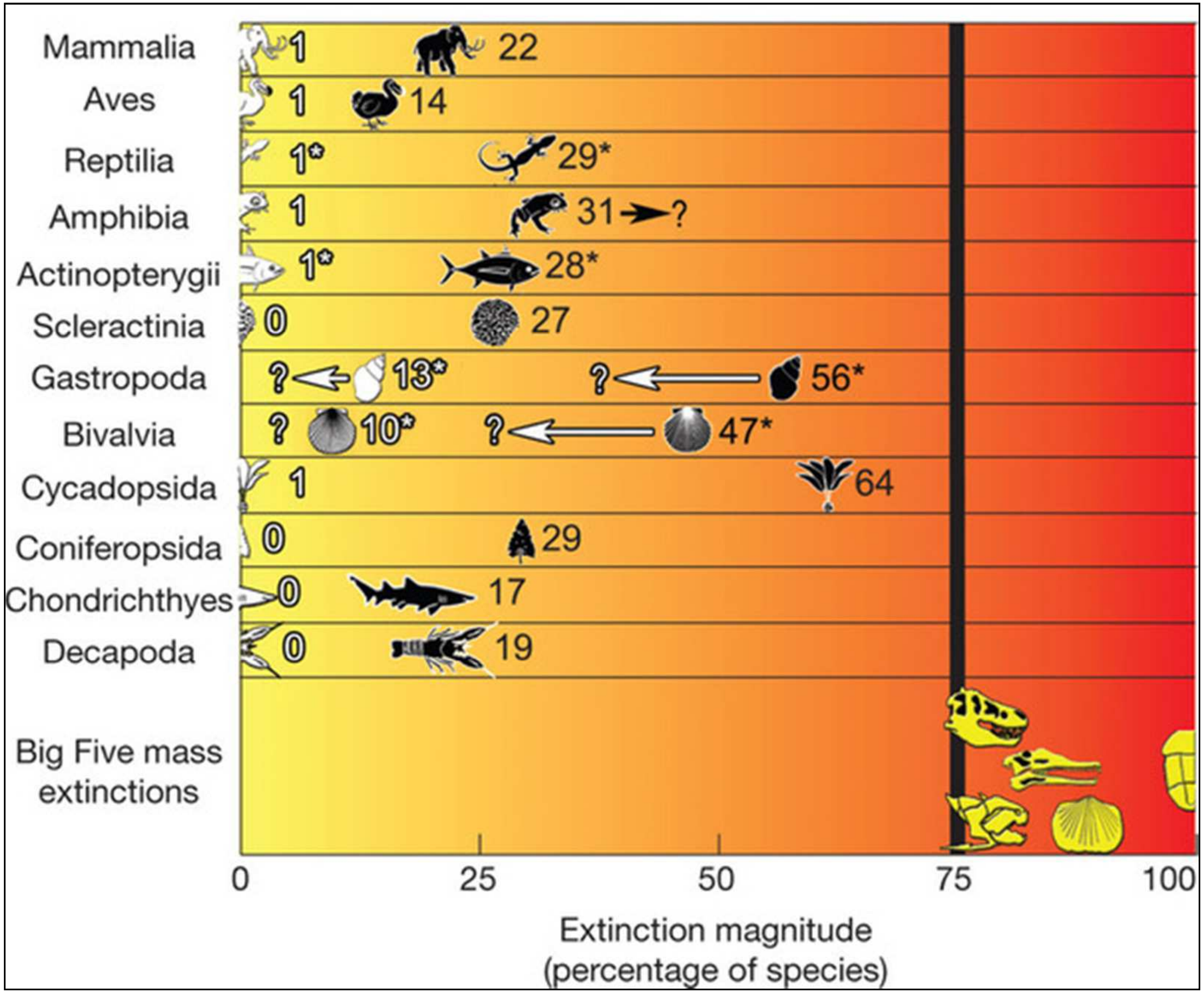
Anthony D. Barnosky[1,2,3], Nicholas Matzke[1], Susumu Tomiya[1,2,3], Guinevere O. U. Wogan[1,3], Brian Swartz[1,2], Tiago B. Quental[1,2]†, Charles Marshall[1,2], Jenny L. McGuire[1,2,3]†, Emily L. Lindsey[1,2], Kaitlin C. Maguire[1,2], Ben Mersey[1,4] & Elizabeth A. Ferrer[1,2]

3 MARCH 2011 | VOL 471 | NATURE | 51

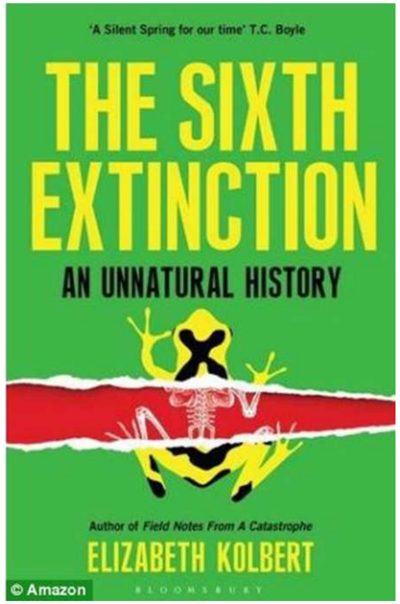
- Accelerated climate dynamics? YES
- Changes in atmospheric composition? YES
- Abnormally high-intensity ecological stressors? YES.

= Magnitude and rate of anthropic mass extinction in comparison with the Big Five: over the past 500 years, from 22% in mammalia to 47-56% in gastropoda and bivalvia.

"Our results confirm that current extinction rates are higher than would be expected from the fossil record. … The Earth could reach the extreme rates of the Big Five mass extinctions within just few centuries if current threats to many species are not alleviated".



Barnosky et al., 2011, *Nature*, 471: 51-57.



Defaunation in the Anthropocene
Rodolfo Dirzo *et al.*
Science **345**, 401 (2014);
DOI: 10.1126/science.1251817

REVIEW

Defaunation in the Anthropocene

Rodolfo Dirzo,[1*] Hillary S. Young,[2] Mauro Galetti,[3] Gerardo Ceballos,[4] Nick J. B. Isaac,[5] Ben Collen[6]

We live amid a global wave of anthropogenically driven biodiversity loss: species and population extirpations and, critically, declines in local species abundance. Particularly, human impacts on animal biodiversity are an under-recognized form of global environmental change. Among terrestrial vertebrates, 322 species have become extinct since 1500, and populations of the remaining species show 25% average decline in abundance. Invertebrate patterns are equally dire: 67% of monitored populations show 45% mean abundance decline. Such animal declines will cascade onto ecosystem functioning and human well-being. Much remains unknown about this "Anthropocene defaunation"; these knowledge gaps hinder our capacity to predict and limit defaunation impacts. Clearly, however, defaunation is both a pervasive component of the planet's sixth mass extinction and also a major driver of global ecological change.

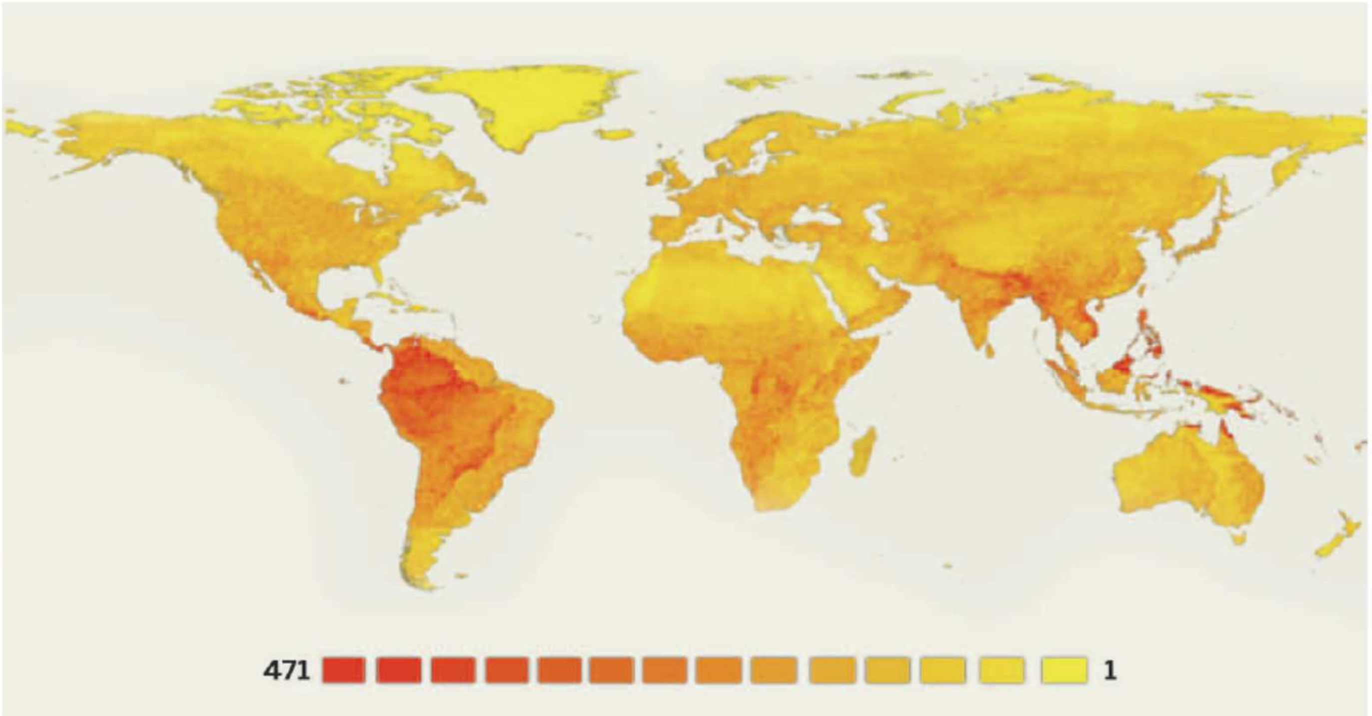


Fig. 2. Global population declines in mammals and birds. The number of species defined by IUCN as currently experiencing decline, represented in numbers of individuals per 10,000 km^2 for mammals and birds, shows profound impacts of defaunation across the globe.

Earth's Sixth Mass Extinction Event☆

T Pievani, University of Padua, Padova, Italy

Rend. Fis. Acc. Lincei
DOI 10.1007/s12210-013-0258-9

ANTHROPOCENE - NATURAL AND MAN-MADE ALTERATIONS OF THE EARTH

The sixth mass extinction: Anthropocene and the human impact on biodiversity

Telmo Pievani

We are not in the middle of a sixth mass extinction yet, but all the conditions are there (we are in the extinction trajectory, with accelerating rates): ANTHROPOCENE

What the evolutionary role of mass extinctions?

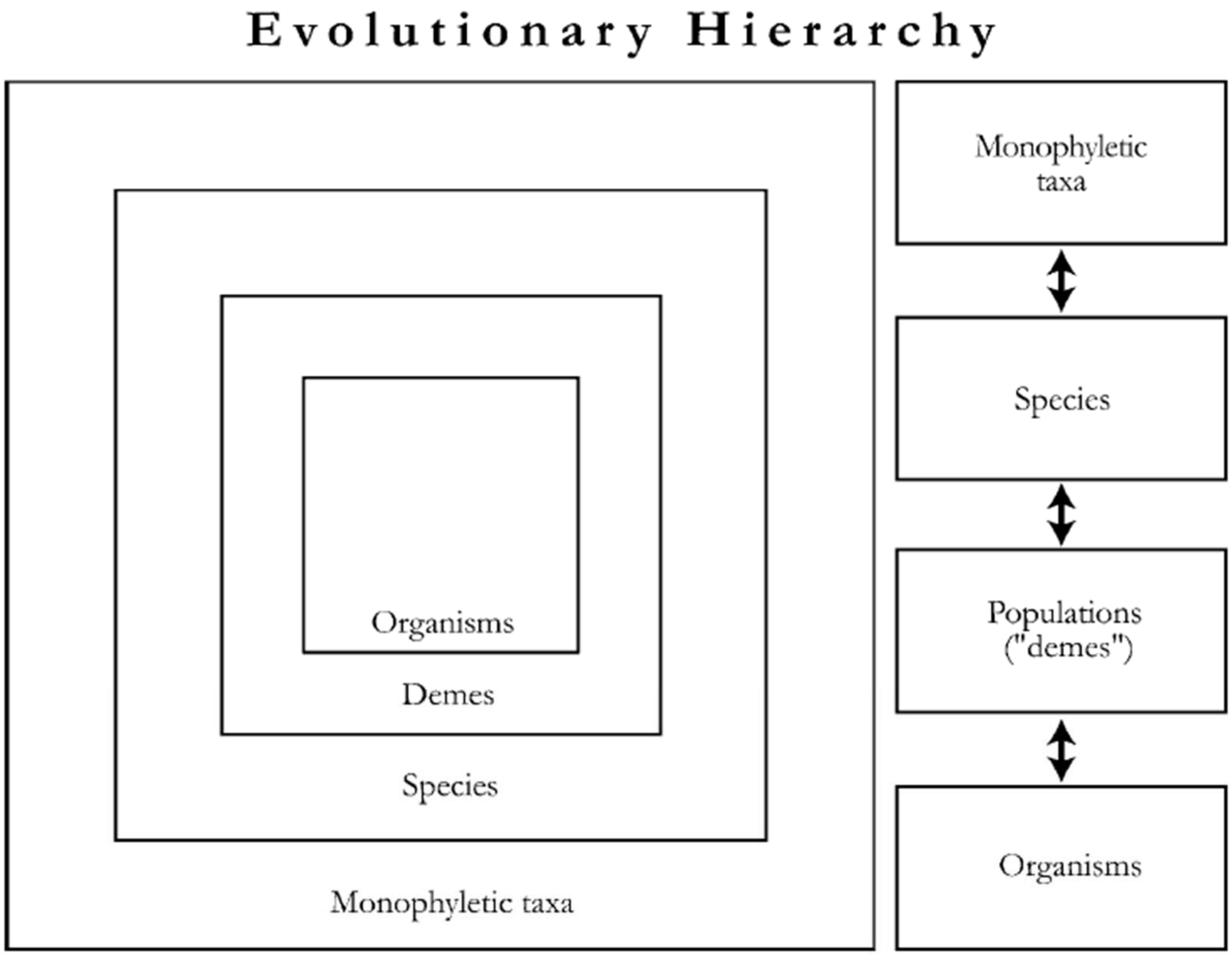


Fig. 1 The evolutionary hierarchy

Niles Eldredge (2008) , "Hierarchies and the Sloshing Bucket: Toward the Unification of Evolutionary Biology", in *Evo Edu Outreach* 1 pp. 10–15.

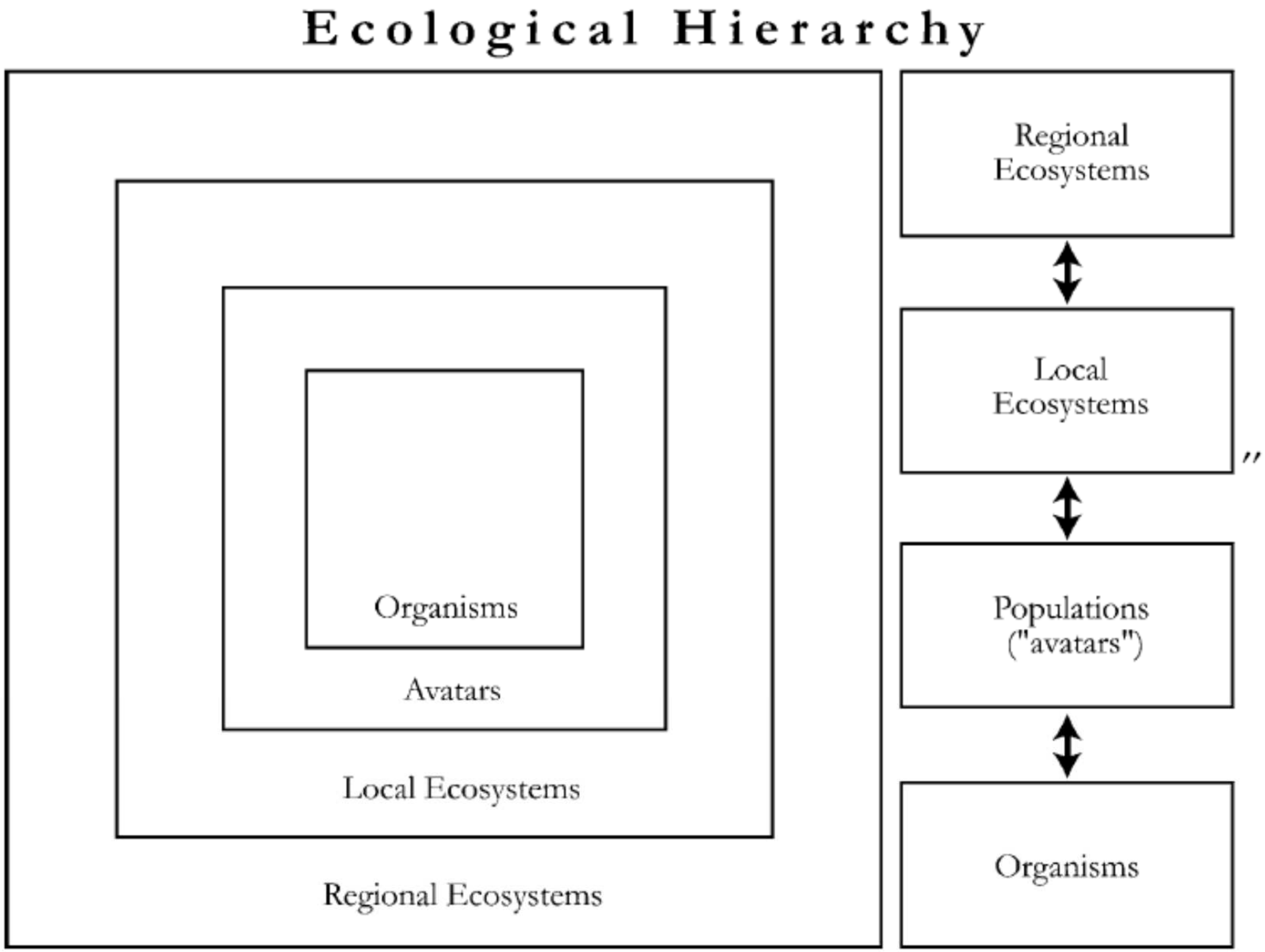


Fig. 2 The ecological hierarchy

Niles Eldredge (2008) , “Hierarchies and the Sloshing Bucket: Toward the Unification of Evolutionary Biology”, in *Evo Edu Outreach* 1 pp. 10–15.

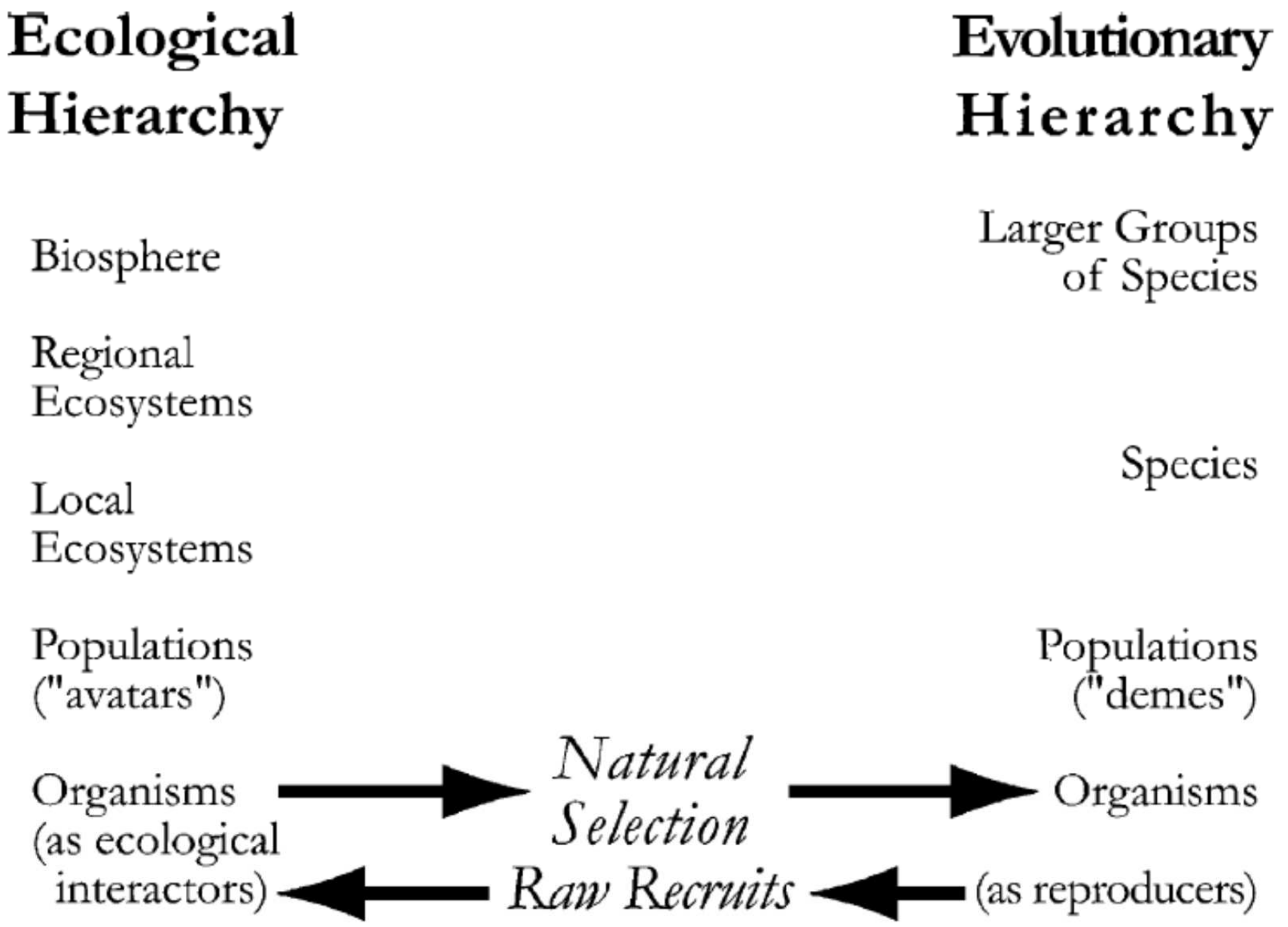


Fig. 3 The two hierarchies and natural selection

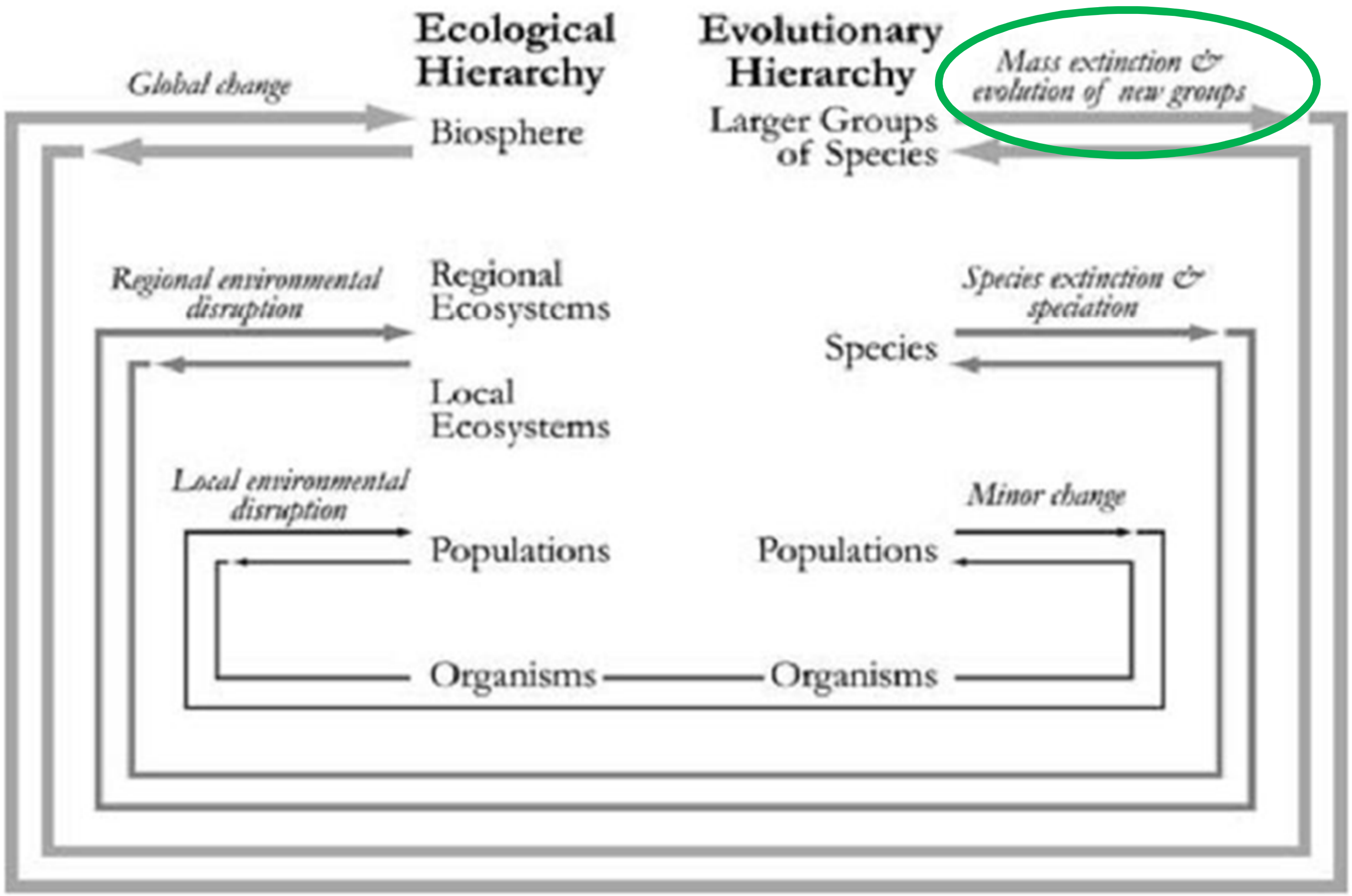
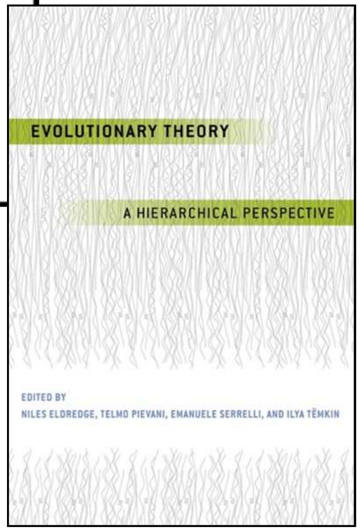


Fig. 4 The sloshing bucket theory of evolution



Unifying pattern for macro-evolution

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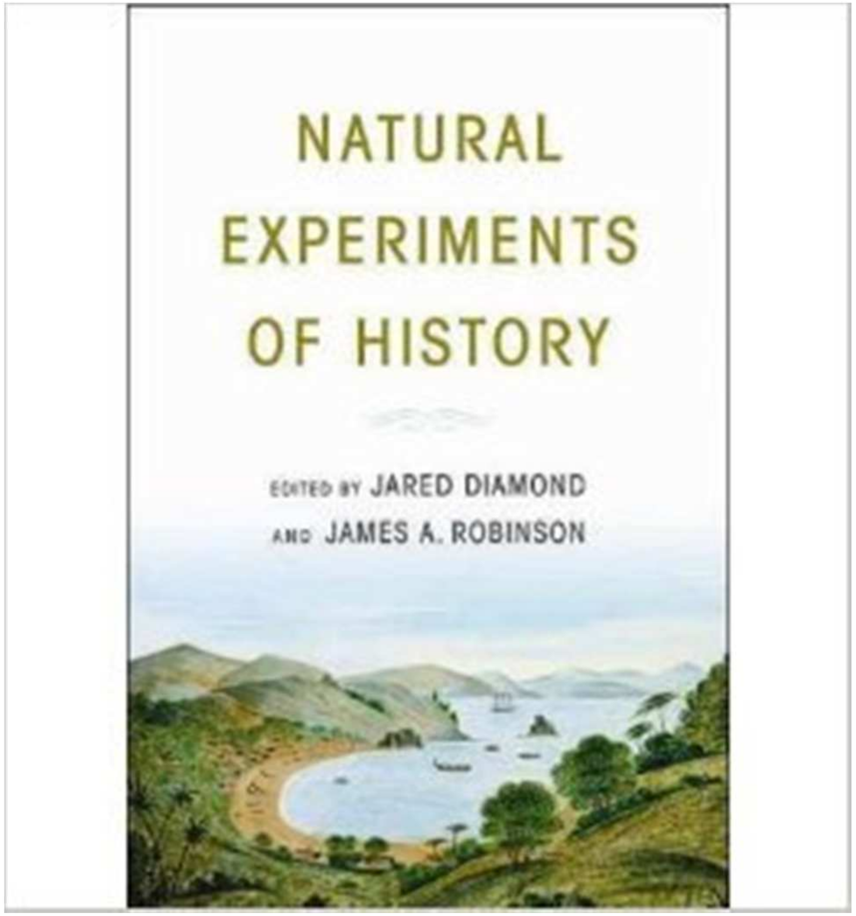
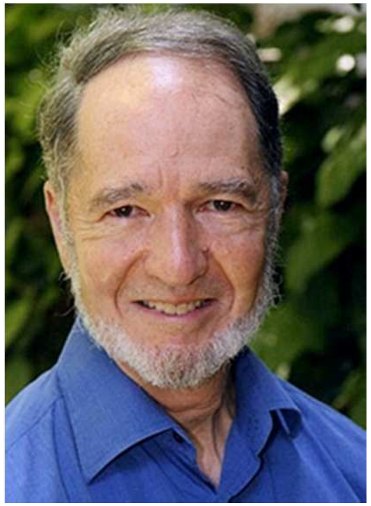
3. Historical «experiments» and patterns





Jared Diamond

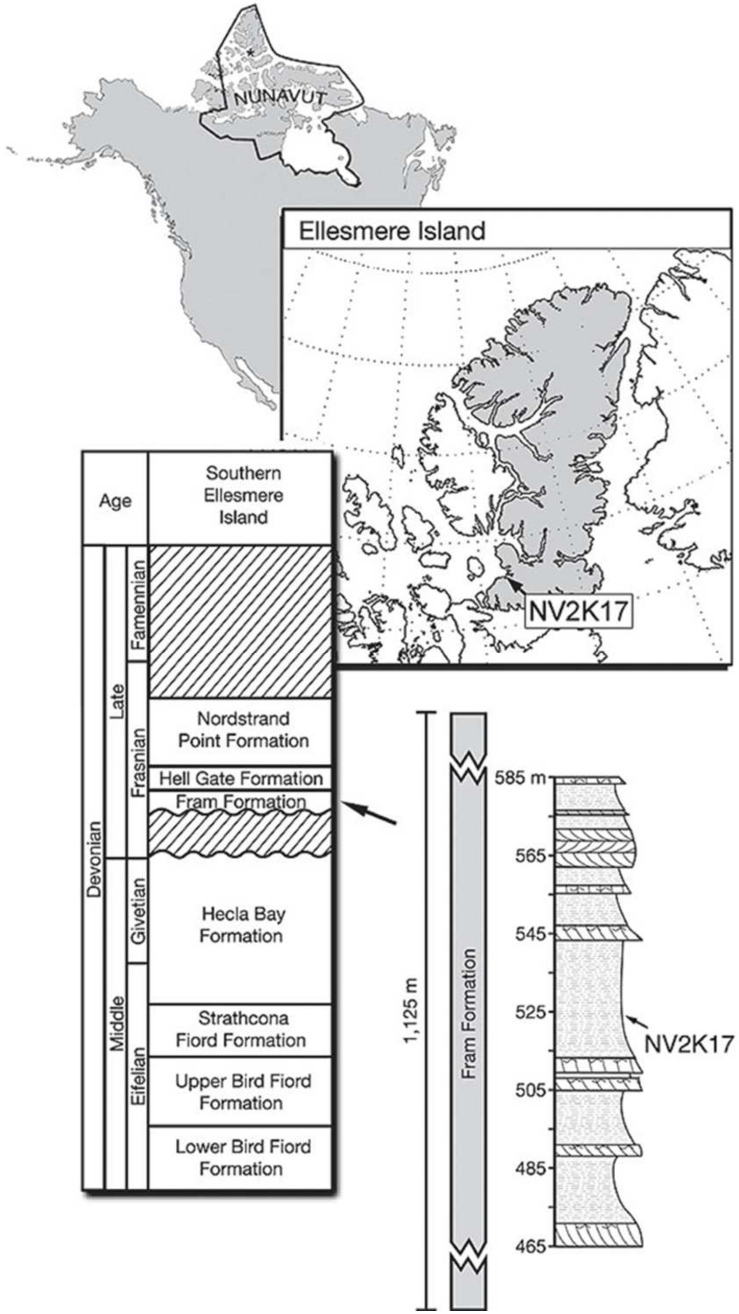
- Same ecological conditions, different cultural pathways (contingent historical divergences)

- Same bio-cultural origin, different social pathways (due to divergent ecological conditions)

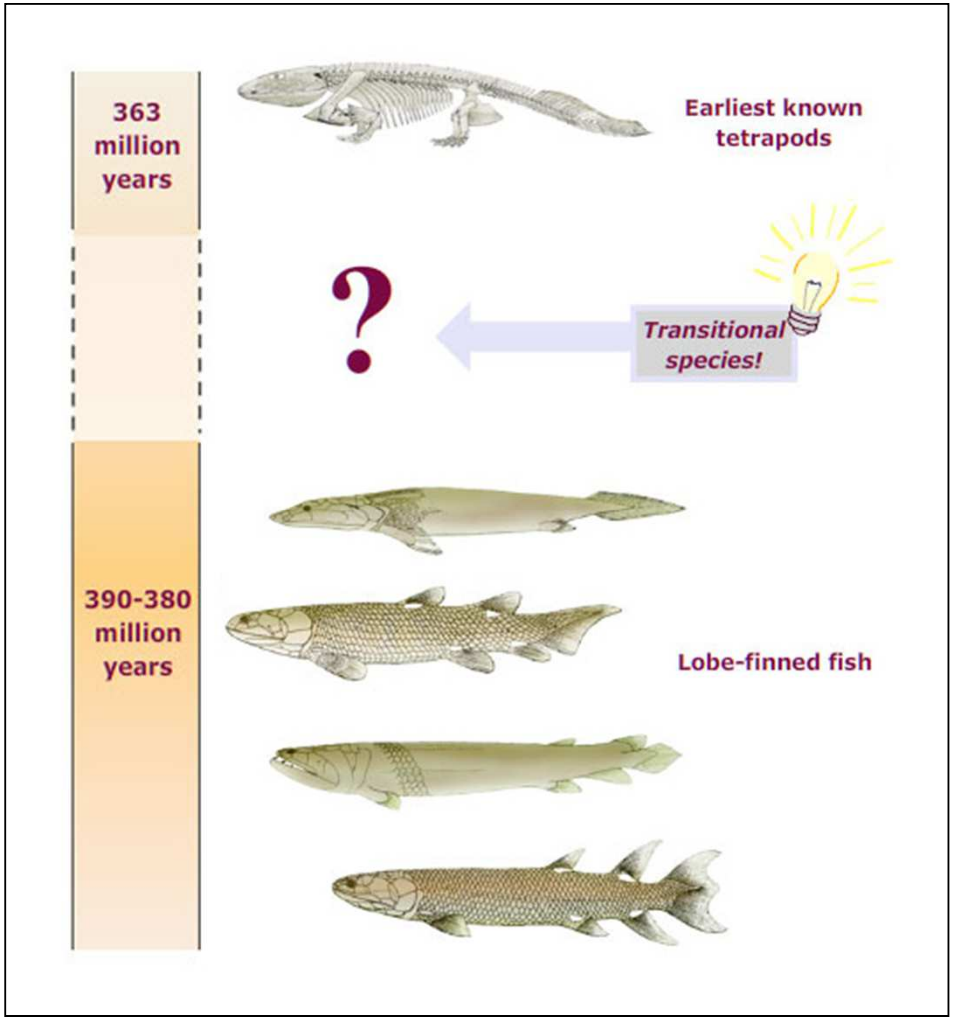
"Historical science is not worse, more restricted, or less capable of achieving firm conclusions because experiment, prediction, and subsumption under invariant laws of nature do not represent its usual working methods. The sciences of history use a different mode of explanation, rooted in the comparative and observational richness of our data"

(S.J. Gould, 1989, p. 274).

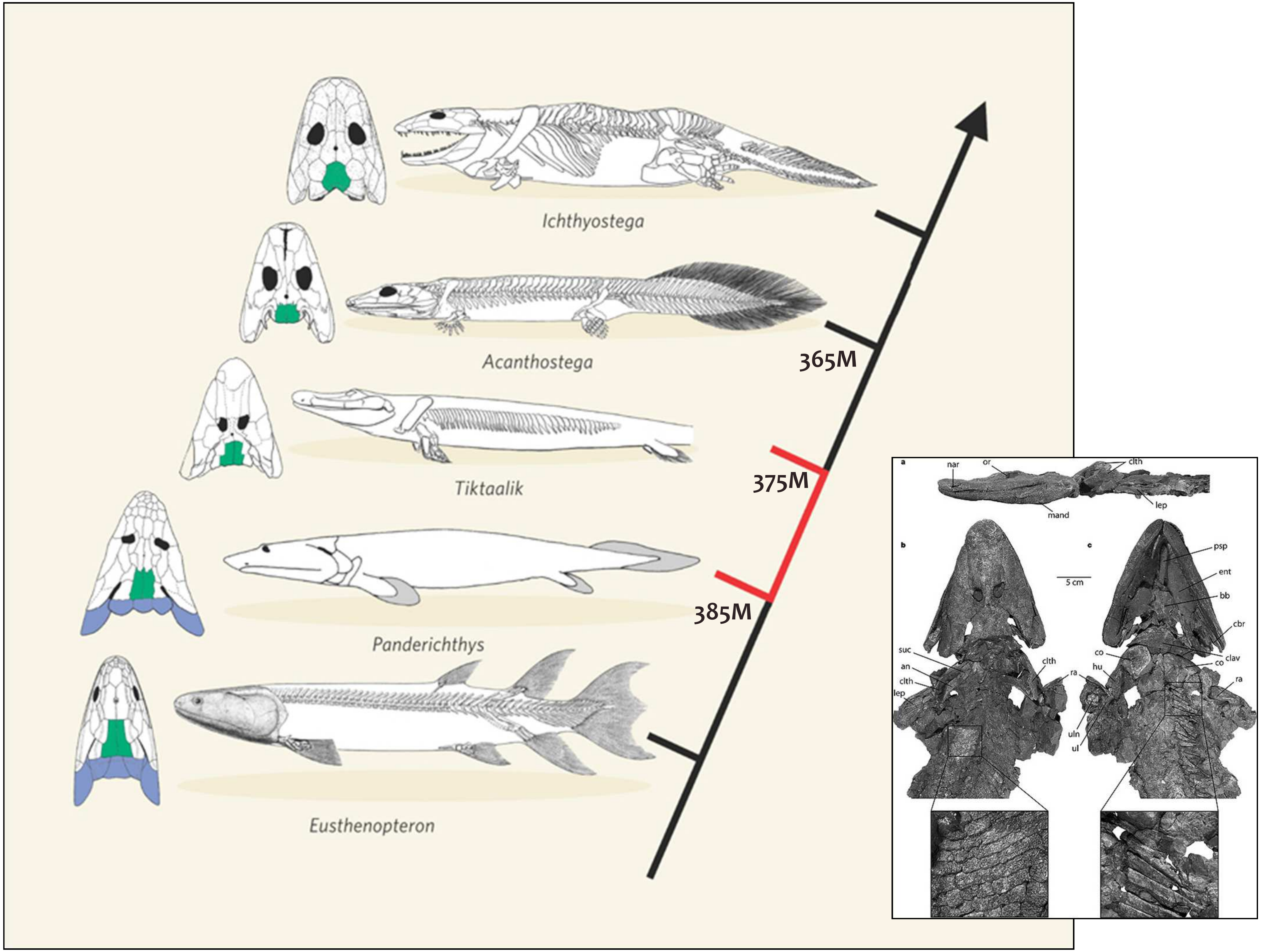
Retrodictions and… predictions



“Scientific theories are powerful because they allow us to make predictions about our world. We look at all the evidence we have gathered to date and predict what we might find if we do certain experiments. If the results of these experiments confirm our predictions, we know we have a solid theory. If not, we revise our theory and keep asking questions. As paleontologists, we can't go to a lab and use beakers and test tubes to gather evidence to test our theories. Instead, we look at the fossil evidence that exists today to make predictions about what we might find in the field tomorrow”.



http://tiktaalik.uchicago.edu/searching4Tik.html



Ichthyostega
Acanthostega
365M
Tiktaalik
375M
385M
Panderichthys
Eusthenopteron
a
nar
or
clth
mand
lep
b
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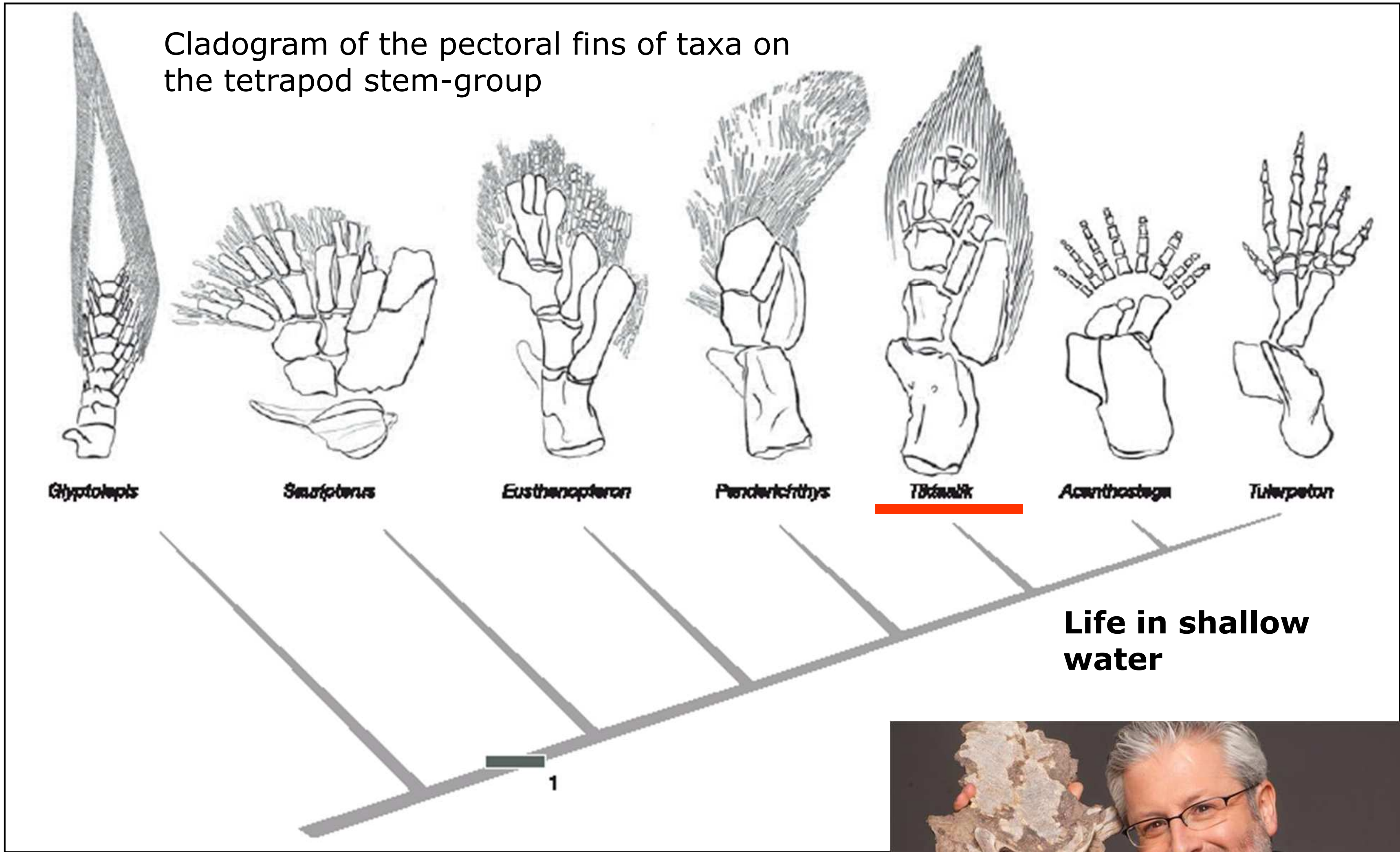
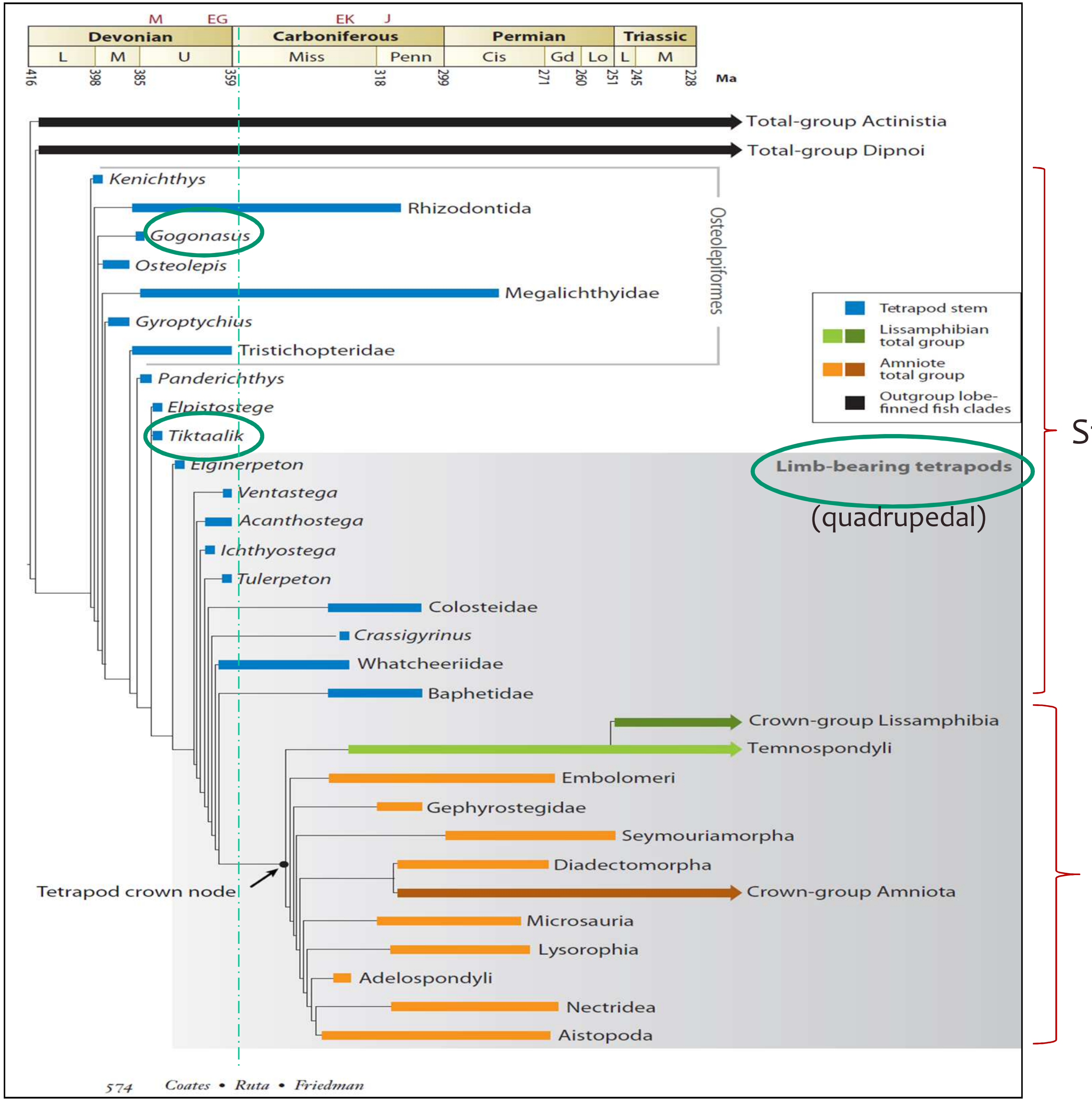


Cladogenetic pattern
+
convergent evidence
= prediction

Coates *et al.* 2008, review.

EARLY-TETROPODS PHYLOGENY



This is Tiktaalik.
It is a transitional fossil.
Now shut up.

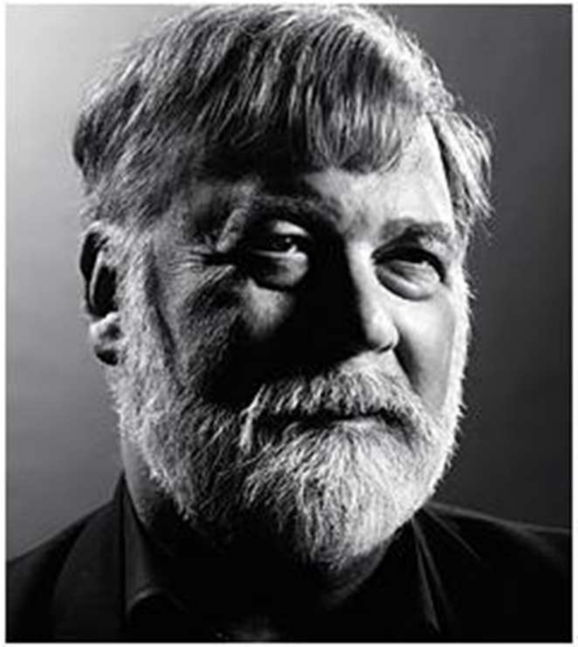
Developmental plasticity and the origin of tetrapods

Emily M. Standen[1], Trina Y. Du[2] & Hans C. E. Larsson[2]

Nature, Sept. 2014

The origin of tetrapods from their fish antecedents, approximately 400 million years ago, was coupled with the origin of terrestrial locomotion and the evolution of supporting limbs. *Polypterus* is a member of the basal-most group of ray-finned fish (actinopterygians) and has many plesiomorphic morphologies that are comparable to elpistostegid fishes, which are stem tetrapods. *Polypterus* therefore serves as an extant analogue of stem tetrapods, allowing us to examine how developmental plasticity affects the 'terrestrialization' of fish. We measured the developmental plasticity of anatomical and biomechanical responses in *Polypterus* reared on land. Here we show the remarkable correspondence between the environmentally induced phenotypes of terrestrialized *Polypterus* and the ancient anatomical changes in stem tetrapods, and we provide insight into stem tetrapod behavioural evolution. Our results raise the possibility that environmentally induced developmental plasticity facilitated the origin of the terrestrial traits that led to tetrapods.

Deep Time and Lab!



Niles Eldredge

«Lawlike» patterns

=

repeated schemes of historical events

(due to unifying principles, processes, mechanisms and causes governing the history of life)

So, you can derive nomothetic principles from the study of contingent histories

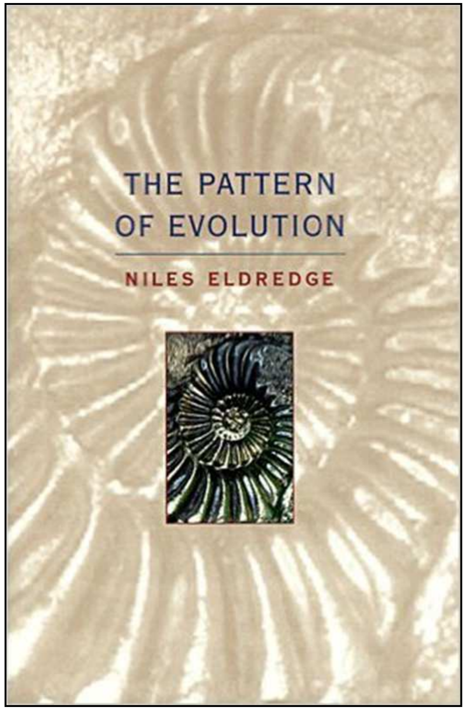
Patterns are:

1. regularities in historical phenomena
(ex. adaptation by natural selection, geographic speciation, turnover pulses, mass-extinctions…);

1. limited in range;

2. with deviations and exceptions;

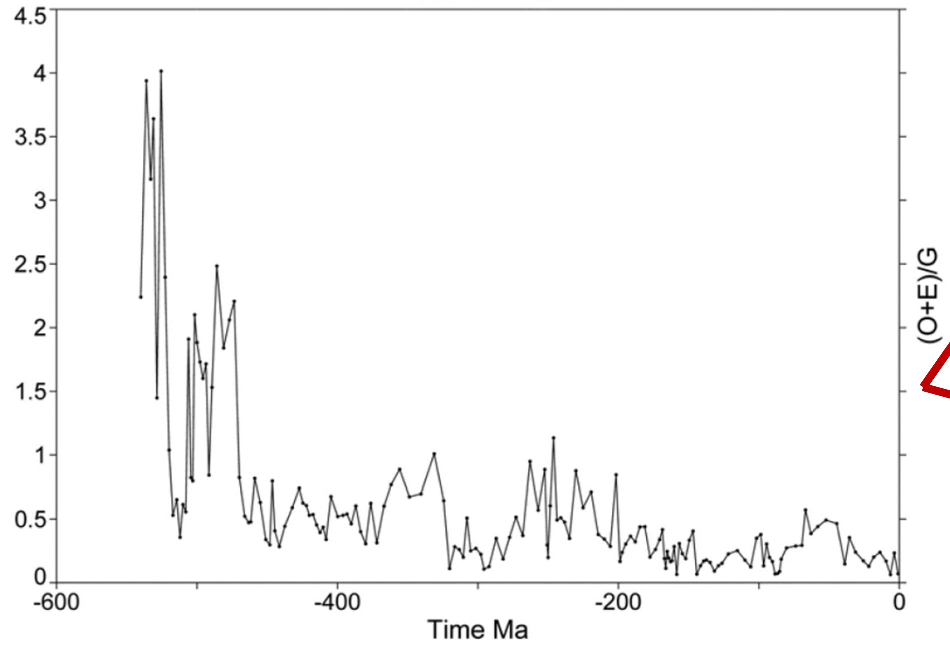
3. phenomena can embody multiple patterns (antagonistic, complementary, integrative).

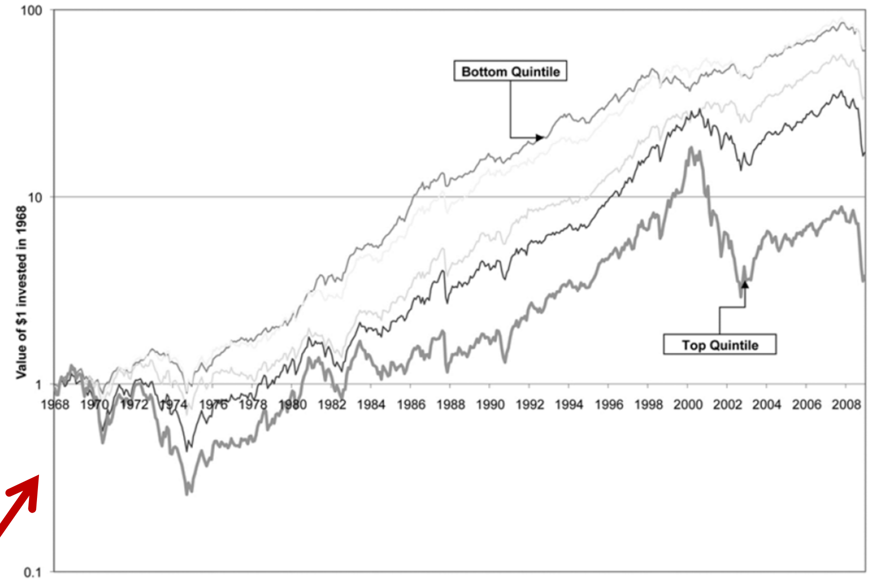


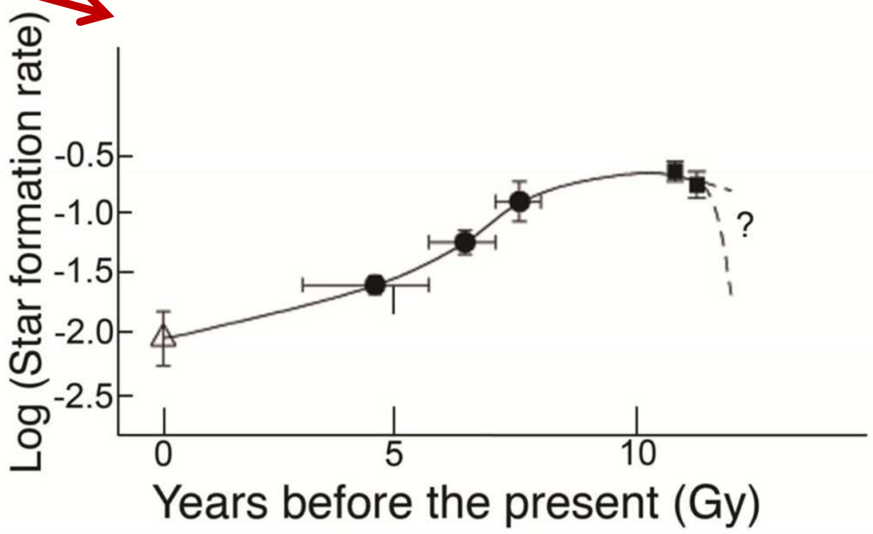
"History is a natural experiment, but also it is a connected sequence of unique events"
(Eldredge, 1989, p. 8)

DECLINING VOLATILITY, A GENERAL PROPERTY OF DISPARATE SYSTEMS: FROM FOSSILS, TO STOCKS, TO THE STARS

by BRUCE S. LIEBERMAN[1] *and* ADRIAN L. MELOTT[2]
[1]Department of Ecology & Evolutionary Biology and Biodiversity Institute; e-mail: blieber@ku.edu
[2]Department of Physics and Astronomy; e-mail: melott@ku.edu
University of Kansas, Lawrence, KS 66045, U.S.A.







Rate of origination and extinction of genera through time:

PATTERN OF DECLINING VOLATILITY

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4. Pluralism of patterns

Philosophy of Selection (Natural, Sexual and Drift)

Telmo Pievani, *Department of Biology, University of Padua, Padua, Italy*

Introductory article

Article Contents

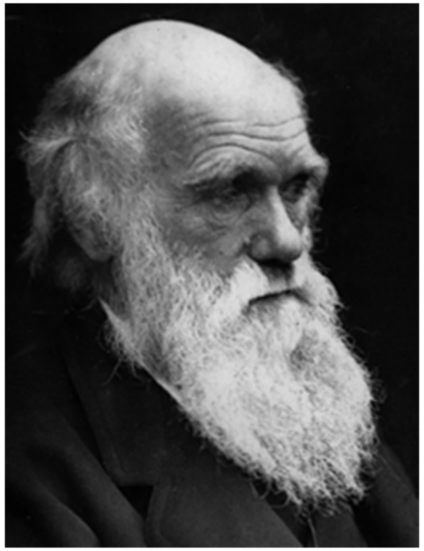
Online posting date: 15th April 2015

Incompatible patterns, together?

Obs. 1: Exponential growth of populations

Obs. 2: The balance of populations

Obs. 3: Limited resources



Ded. 1: Struggle for existence

Obs. 4: Individual diversity

Obs. 5: Heredity of a part of the individual variation

Obs. 6: Variation is not externally directed

Ded. 2: Differential survival

Ded. 3: Differential reproductive success, over generations: change within populations.

Ded. 4: (Principle of divergence) Descent with Modifications

NATURAL SELECTION: SAME INITIAL CONDITIONS (selective pressures) likely imply SAME FUNCTIONAL RESULTS. But…

EVOLUTION

Predictable convergence in hemoglobin function has unpredictable molecular underpinnings

Chandrasekhar Natarajan,[1] Federico G. Hoffmann,[2] Roy E. Weber,[3] Angela Fago,[3] Christopher C. Witt,[4] Jay F. Storz[1]*

To investigate the predictability of genetic adaptation, we examined the molecular basis of convergence in hemoglobin function in comparisons involving 56 avian taxa that have contrasting altitudinal range limits. Convergent increases in hemoglobin-oxygen affinity were pervasive among high-altitude taxa, but few such changes were attributable to parallel amino acid substitutions at key residues. Thus, predictable changes in biochemical phenotype do not have a predictable molecular basis. Experiments involving resurrected ancestral proteins revealed that historical substitutions have context-dependent effects, indicating that possible adaptive solutions are contingent on prior history. Mutations that produce an adaptive change in one species may represent precluded possibilities in other species because of differences in genetic background.

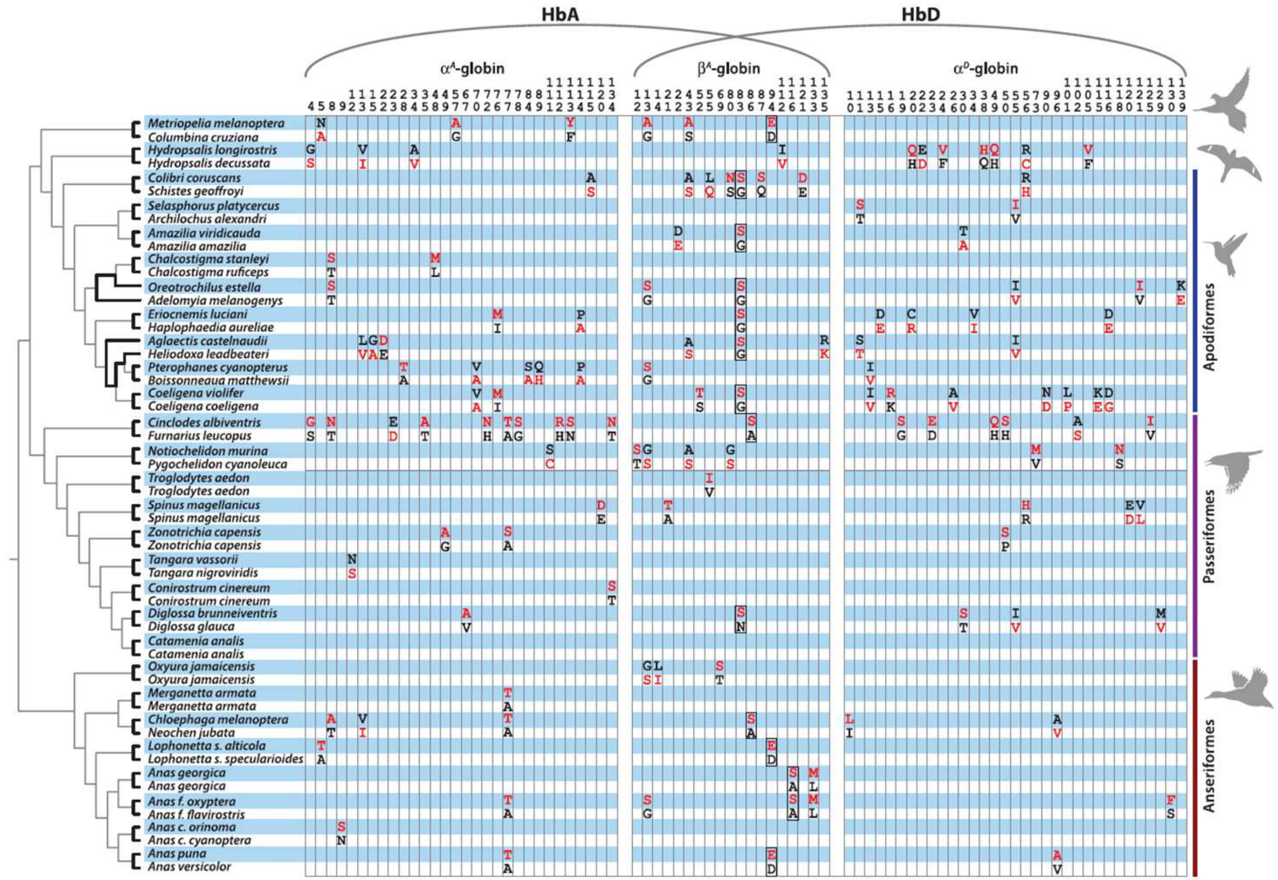


Fig. 1. Amino acid differences that distinguish the Hbs of each pair of high- and low-altitude taxa. Derived (nonancestral) amino acids are shown in red lettering, and rows corresponding to high-altitude taxa are shaded in blue. Subunits of the major HbA isoform are encoded by the α^A- and β^A-globin genes, whereas those of the minor HbD isoform are encoded by the α^D- and β^A-globin genes. Phylogenetically replicated β-chain replacements that contribute to convergent increases in $Hb\text{-}O_2$ affinity (N/G83S, A86S, D94E, and A116S) are outlined. Single-letter abbreviations for the amino acid residues are as follows: A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; and Y, Tyr.

These findings expose a clear demarcation between the realms of chance and necessity at different hierarchical levels. At the level of biochemical phenotype, and even at the level of functional mechanism, evolutionary changes are highly predictable. At the amino acid level, in contrast, predictability breaks down.

Human expansion *out of Africa* has been accompained by a series of founder effects

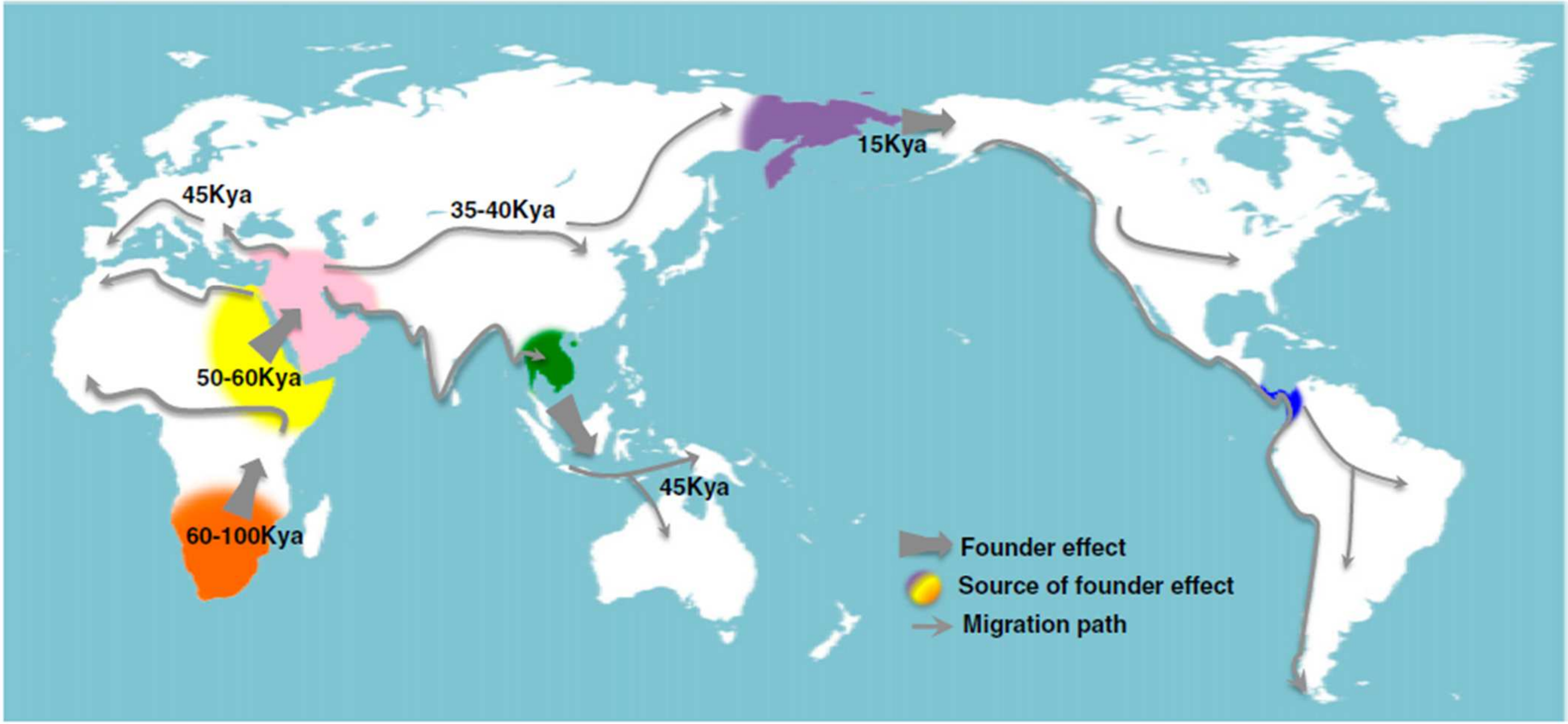


Fig. 1. Ancient dispersal patterns of modern humans during the past 100,000 y. This map highlights demic events that began with a source population in southern Africa 60 to 100 kya and conclude with the settlement of South America approximately 12 to 14 kya. Wide arrows indicate major founder events during the demographic expansion into different continental regions. Colored arcs indicate the putative source for each of these founder events. Thin arrows indicate potential migration paths. Many additional migrations occurred during the Holocene (11).

B. M. Henna, L. L. Cavalli-Sforza, & M. W. Feldman The great human expansion *PNAS*, 109 (44), 17758–17764, 2012

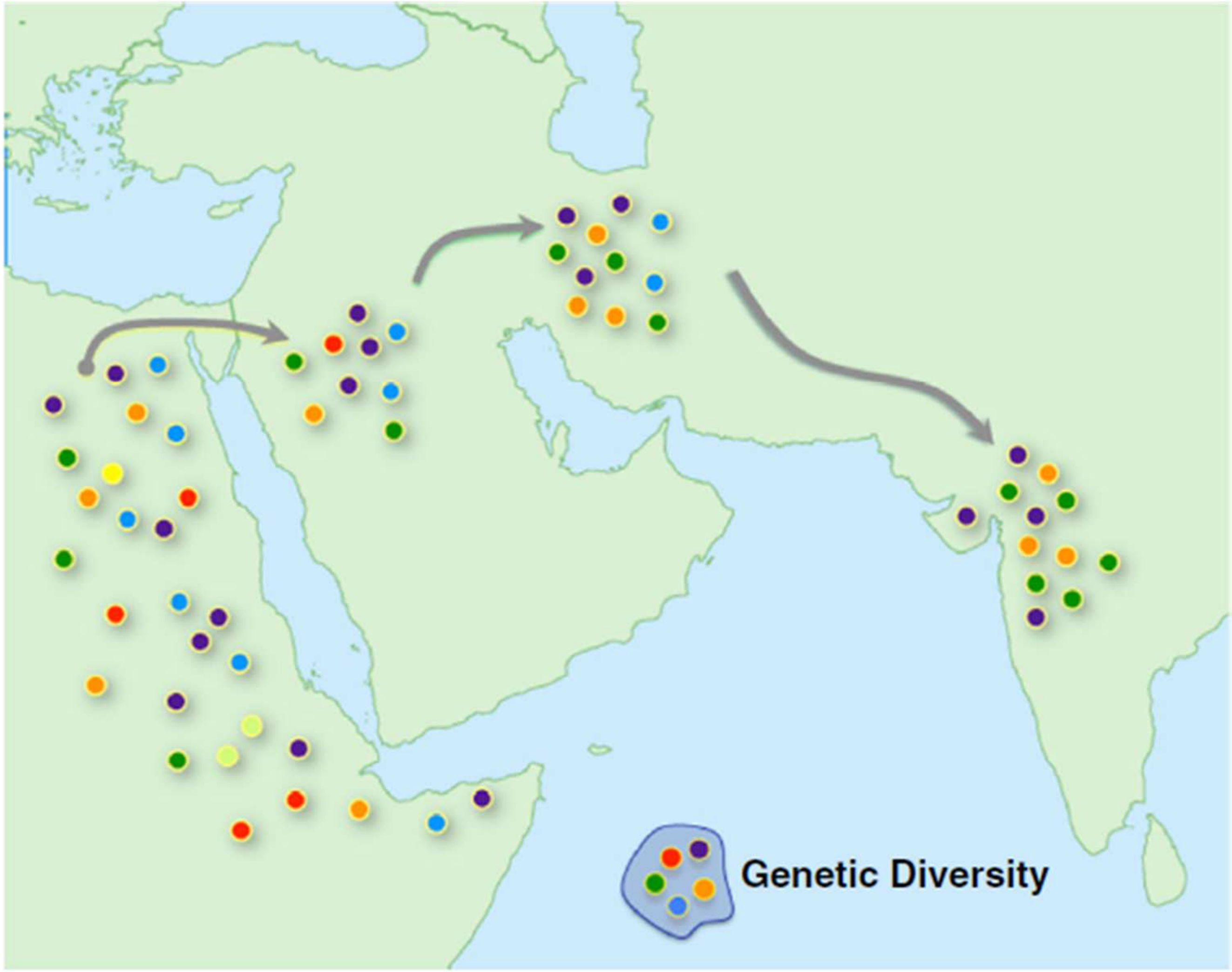
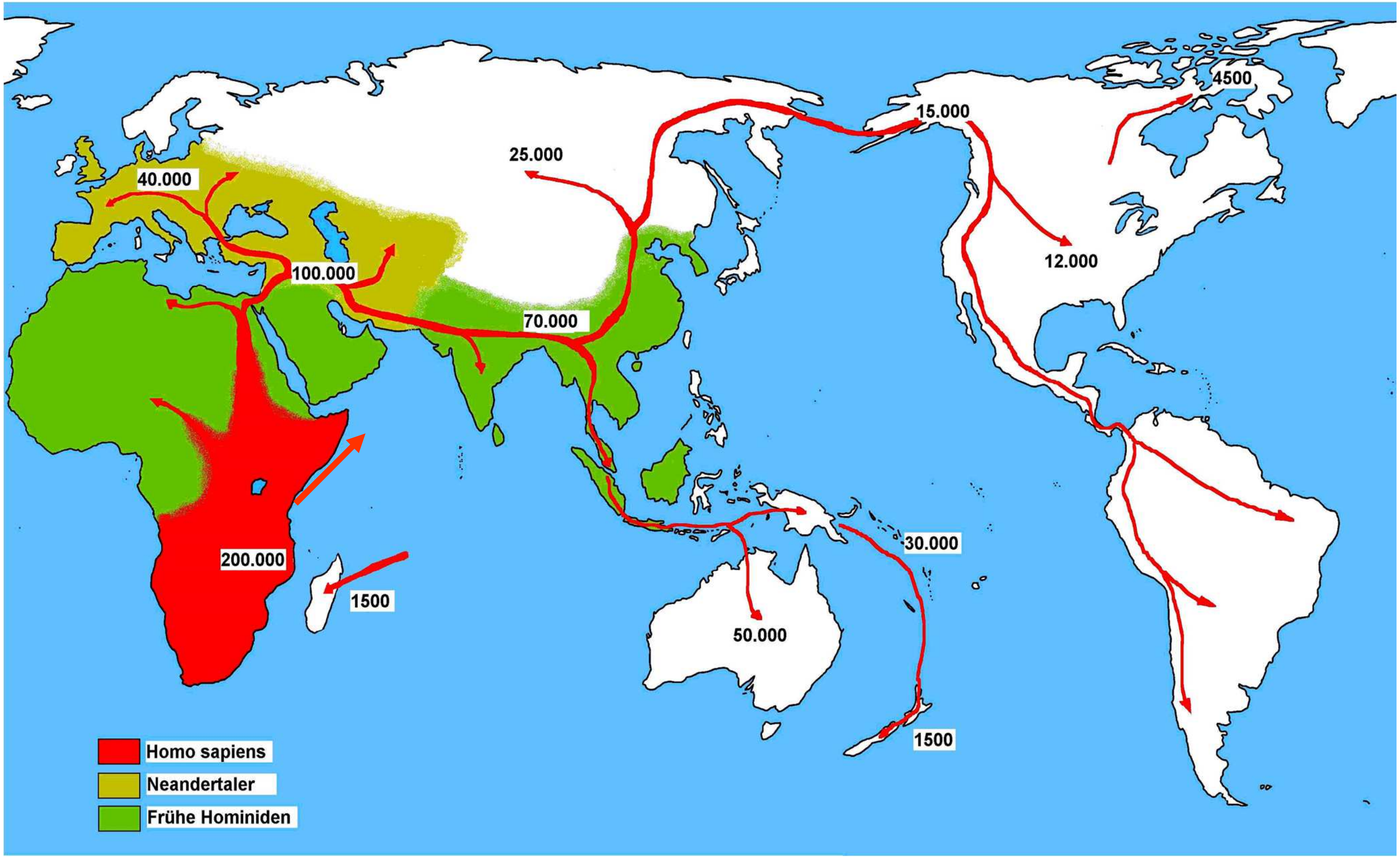


Fig. 2. Schematic of a serial found effect. We illustrate the effect of serial founder events on genetic diversity in the context of the OOA expansion. Colored dots indicate genetic diversity. Each new group outside of Africa represents a sampling of the genetic diversity present in its founder population. The ancestral population in Africa was sufficiently large to build up and retain substantial genetic diversity.

B. M. Henna, L. L. Cavalli-Sforza, & M. W. Feldman The great human expansion *PNAS*, 109 (44), 17758–17764, 2012



RANDOM GENETIC PROCESSES (NO NATURAL SELECTION) PRODUCE VERY PREDICTABLE AND LAW-LIKE PATTERNS!

Complementary patterns

Ex. problem:

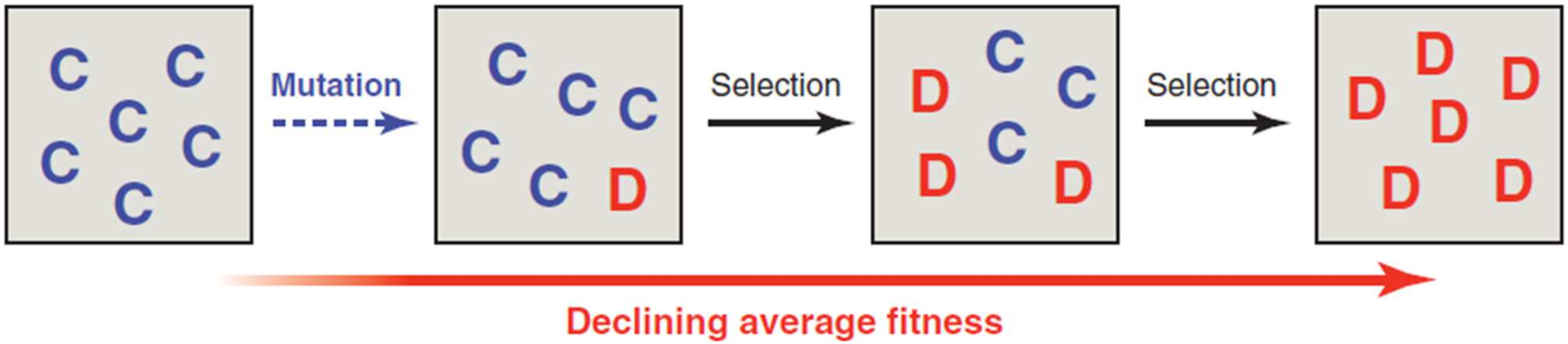
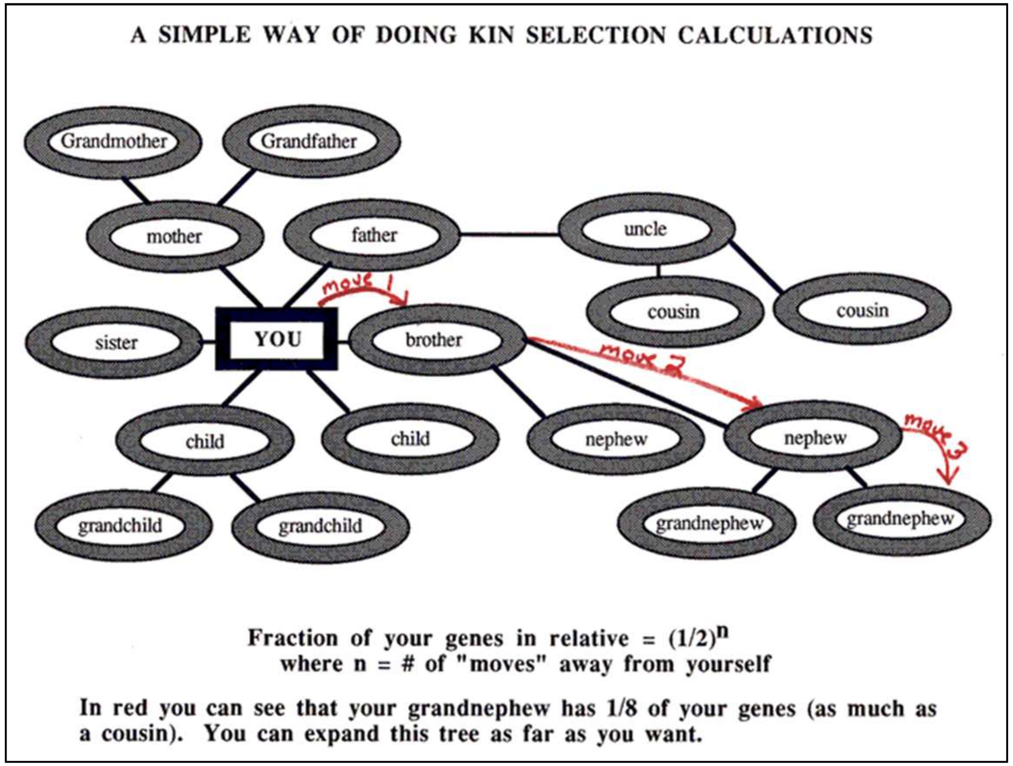
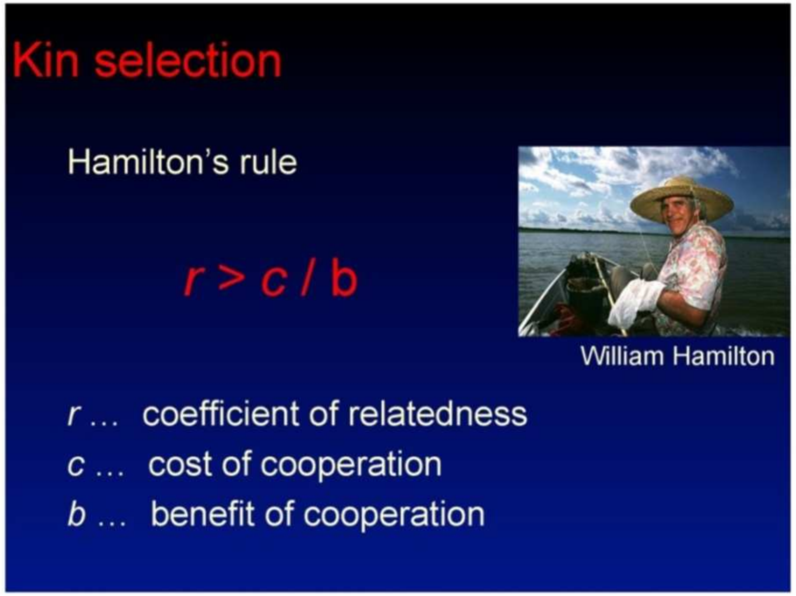


Fig. 1. Without any mechanism for the evolution of cooperation, natural selection favors defectors. In a mixed population, defectors, D, have a higher payoff (= fitness) than cooperators, C. Therefore, natural selection continuously reduces the abundance, i, of cooperators until they are extinct. The average fitness of the population also declines under natural selection. The total population size is given by N. If there are i cooperators and $N - i$ defectors, then the fitness of cooperators and defectors, respectively, is given by $f_C = [b(i-1)/(N-1)] - c$ and $f_D = bi/(N-1)$. The average fitness of the population is given by $\bar{f} = (b - c)i/N$.



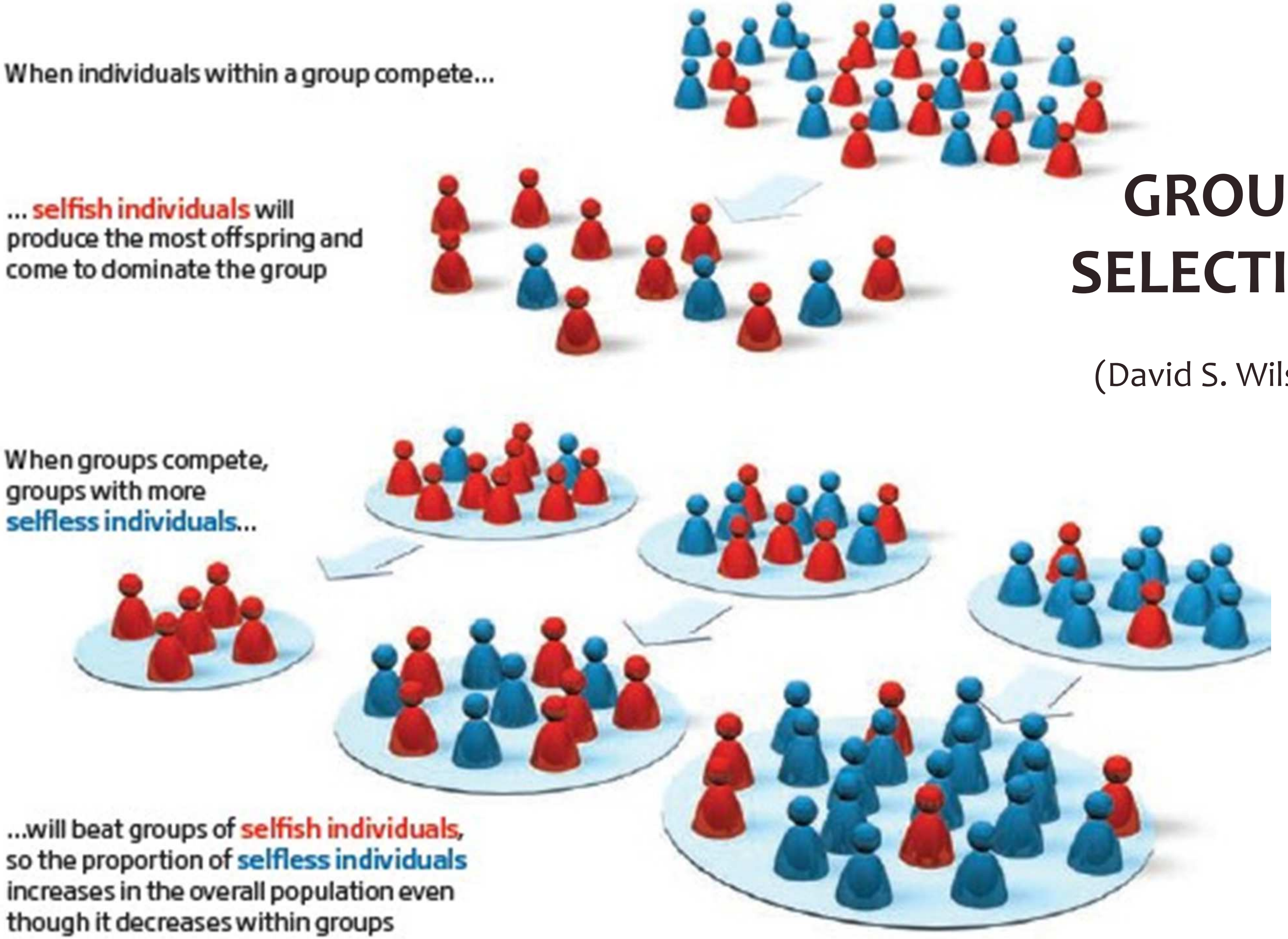
KIN SELECTION

(J.B.S. Haldane, William Hamilton)



GROUP SELECTION

(David S. Wilson)



Large Punctuational Contribution of Speciation to Evolutionary Divergence at the Molecular Level

Mark Pagel,* Chris Venditti, Andrew Meade

A long-standing debate in evolutionary biology concerns whether species diverge gradually through time or by punctuational episodes at the time of speciation. We found that approximately 22% of substitutional changes at the DNA level can be attributed to punctuational evolution, and the remainder accumulates from background gradual divergence. Punctuational effects occur at more than twice the rate in plants and fungi than in animals, but the proportion of total divergence attributable to punctuational change does not vary among these groups. Punctuational changes cause departures from a clock-like tempo of evolution, suggesting that they should be accounted for in deriving dates from phylogenies. Punctuational episodes of evolution may play a larger role in promoting evolutionary divergence than has previously been appreciated.

The theory of punctuated equilibrium as a description of evolution suggests that evolutionary divergence among species is characterized by long periods of stability or stasis followed by short punctuational bursts of evolution associated with speciation. Despite years of work on punctuational change, the theory remains contentious (*1–9*), with little or no consensus as to the contribution of punctuational changes to evolutionary divergence. The importance of the theory lies in the challenge it poses for classical accounts of how species diverge.

Punctuational evolution has traditionally been studied in the fossil record. However, phylogenetic trees derived from gene-sequence data contain the signatures of past punctuational and gradual evolution and can be used to study their relative contributions to evolutionary divergence (*10*) (Fig. 1). The nodes of a phylogenetic tree record the number of net-speciation events (speciation-extinction) between the root of the tree and the extant species (Fig. 1, A and B). In phylogenies derived from gene-sequence data, the lengths of the branches of the tree record the expected evolutionary divergence between pairs of speciation events, measured in units of nucleotide substitutions. We denote the sum of the branch lengths between the root of the tree and a species as the path length and write this path length as $x = n\beta + g$, where n is the number of nodes along a path, β is the punctuational contribution of speciation to evolution at each node, and g is the gradual contribution to the path, this being the sum of the individual gradual effects in each branch along the path. Both parameters are measured in units of expected nucleotide substitutions per site in the gene-sequence alignment. Under a gradual model of evolution, there is no punctuational effect, $\beta = 0$, and there should be no relationship between x and n (Fig. 1, B and C). If, however, speciation events are associated with bursts of evolution, then $\beta > 0$, and path lengths from the root to the tips of the tree will be correlated with the number of speciation events that occur along that path (Fig. 1, A and C).

We analyzed 122 gene-sequence alignments selected for including a well-characterized and narrow taxonomic range of species (*11*). This acts to control for background differences among species, such as generation times or adaptive radiation of some lineages, that might affect rates of evolution independently of a punctuational effect. For each data set, we derived a Bayesian sample of the posterior distribution of phylogenetic trees (*11*, *12*). We then estimated β from the relationship between x and n in each tree in the posterior sample to account for phylogenetic uncertainty, using a statistical method (*10*, *13–15*) that controls for the shared inheritance of branch lengths implied by the phylogeny (Fig. 1)

Using conservative statistical criteria (*11*), we found a significant relationship between nodes and path lengths (i.e., $\beta > 0$) in 57 [46.7 ± 4.5% (±SE)] of the 122 trees. We removed 22 of these data sets with $\beta > 0$ because they suffered from an artifact of phylogeny reconstruction known as the node-density effect, which can produce an apparent relationship between x and n (*10*, *11*, *16–18*). This left 35.0 ± 4.8% of the remaining 100 trees with significant effects of punctuational evolution (Fig. 2), rising to 55.8 ± 7.0% for trees above the median size of n = 28 taxa. The overall frequency of 35% is similar to that found in the subset of trees in which 50% of the known taxa have been

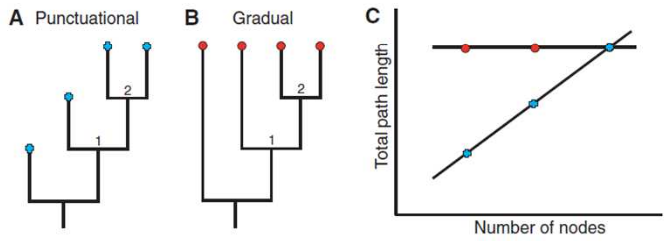


Fig. 1. Signatures of punctuational and gradual evolution on phylogenetic trees. (**A**) Punctuational evolution presumes a burst of evolution associated with each node of the tree. Path lengths, measured as the sum of branches along a path from the root to the tips of the tree, are proportional to the number of nodes along that path (C). Branches are assumed to be in units of nucleotide substitutions. (**B**) Gradual evolution presumes that change is independent of speciation events. Path lengths do not correlate with the number of nodes along a path (C). (**C**) Punctuational evolution predicts a positive relationship between path length and the number of nodes, whereas gradual evolution does not.

School of Biological Sciences, University of Reading, Whiteknights, Reading RG6 6AJ, UK.

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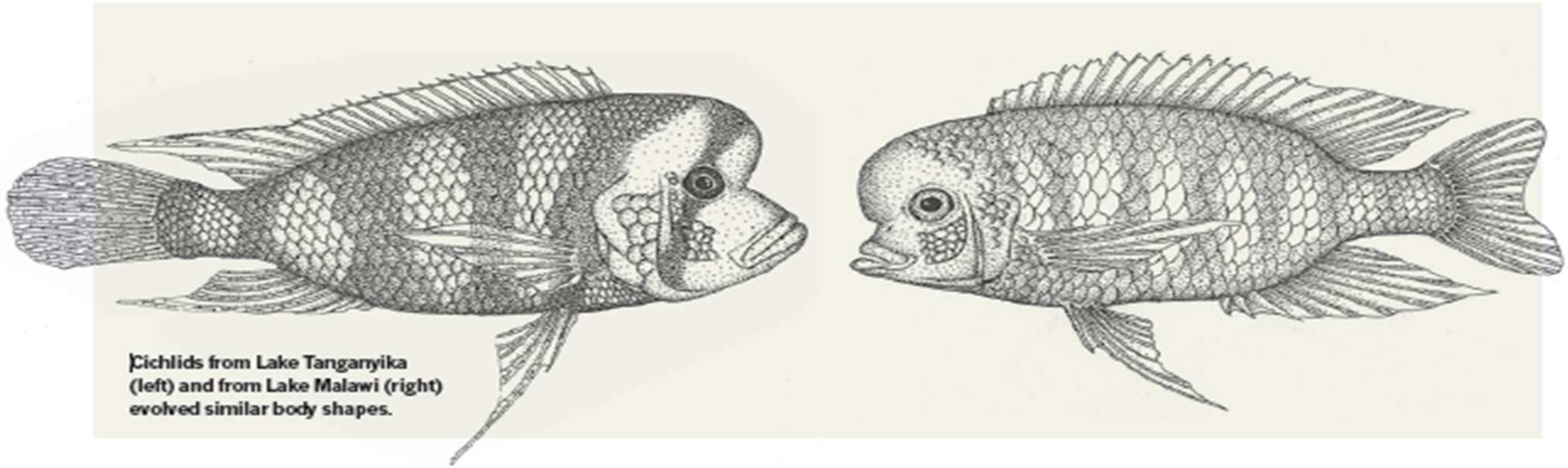
Integrative patterns

GRADUALISM or PUNCTUATIONISM?

Both, and relative frequencies



Cichlids from Lake Tanganyika (left) and from Lake Malawi (right) evolved similar body shapes.

Does evolutionary theory need a rethink?

Researchers are divided over what processes should be considered fundamental.

POINT

Yes, urgently

Without an extended evolutionary framework, the theory neglects key processes, say Kevin Laland *and colleagues.*

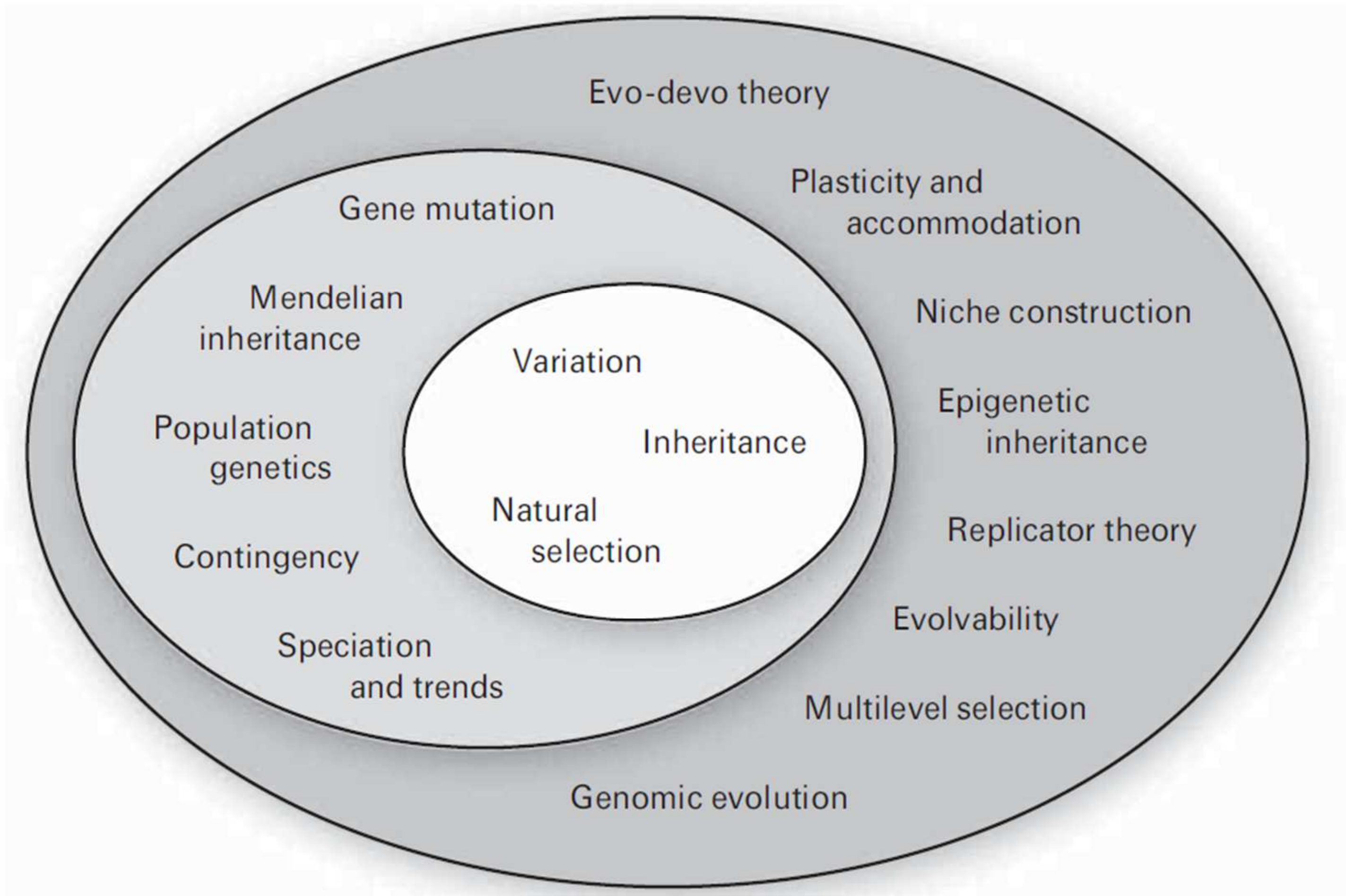
COUNTERPOINT

No, all is well

Theory accommodates evidence through relentless synthesis, say Gregory A. Wray, Hopi E. Hoekstra *and colleagues.*

Nature, Oct. 2014

Meta-pattern: evolutionary research programme



Pigliucci, Muller (eds), *Evolution – The Extended Synthesis*, The MIT Press, 2010

When we come to realize that even among the vertebrates there are 50,000 different 'vertebrate stories', each one with a different ending and each one with a different narrative landscape; when we truly think in terms of the diverging tree, instead of the line; when we understand that it is absurd to talk of one animal being higher than another; only then will we see the full grandeur of the historical view of life.

R.J. O'Hara, 1992, «Telling the Tree»,
Biology&Philosophy.