Punctuations, Stasis & Gradualism

Schedule

T, 1-Dec	Format	Th, 3-Dec	Format	T, 8-Dec	Format
Mariana Gelambi (10 min)	10	Caitlin Carey	10	Fernanda Vasquez-Valverde	15
Alaina Weinheimer (10 min)	10	Guilherme Dalponti	10	Kaitlyn Malewicz	15
Tommy Phannareth	10	Camilo Alfonso	15	Bailey Howell	15
		Carolina Martinez-Gutierrez	15	Erika Goldschmidt	10
		Connor Brown	15	Duke Chiu	10
		Sean McHugh	10		

Presentation rubric

1. Introduce sufficient biological background on research topic
2. Presents a coherent research question with explicit connection made to actual research conducted
3. Methodology explained. Relevant assumptions identified/justified/defended.
4. Data sources and structure described sufficiently.
5. Results correctly interpreted in terms of biological question. (Units, parameters, in understandable, biological terms!)
6. Appropriate model caveats and violated assumptions identified, suggestions for methods that may answer the question better.

Additional components:

1. Well organized and clearly presented (limited amount of text)
2. Timing (lightening or full)
3. Clear and concise delivery

Why is it important to study macroevolution?

Are patterns different between micro and macroevolution?

Are processes different between micro and macroevolution?

Breakout groups: Write down answers to the following questions

1. What processes only operate at macroevolutionary scales?

2. What is Punctuated Equilibrium (PE)?

3. What process generates the pattern? Be as specific as you can about the exact mechanism.

4. What are the implications of PE for our understanding of macroevolution?

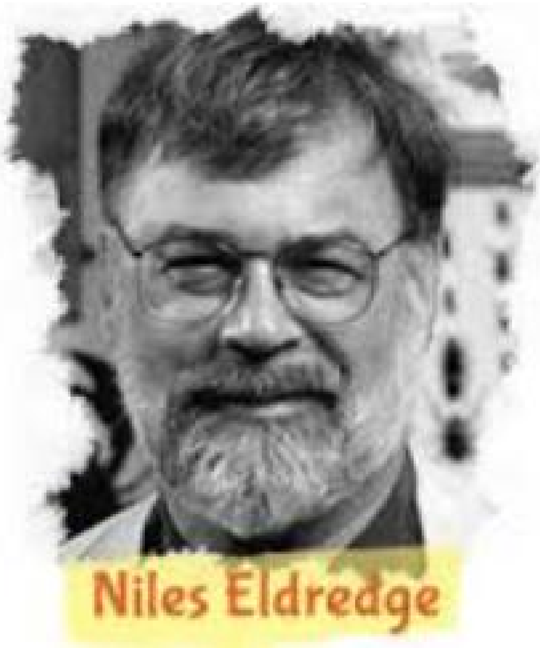
5. Do you think it is controversial? Why or why not?

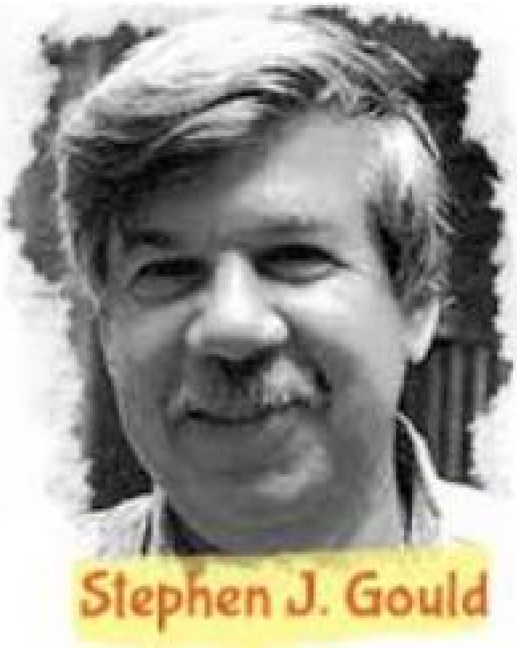
What is the relationship between speciation and trait change?

Is evolution faster in small or large populations?

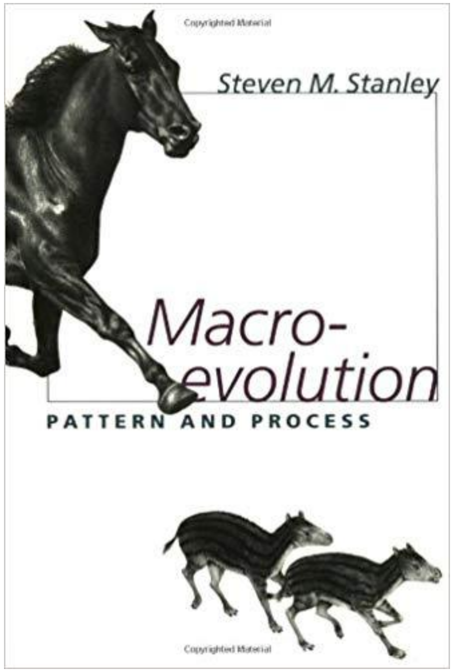
How do micro and macroevolutionary rates compare?

Ernst Mayr - BSC & speciation





'If most evolutionary change occurs during speciation events, and if speciation events are largely random, natural selection, long viewed as the process guiding evolutionary change, cannot play a significant role in determining the overall course of evolution. Macroevolution is decoupled from microevolution...' ([22], p. 648).



(2) Many breaks in the fossil record are real; they express the way in which evolution occurs, not the fragments of an imperfect record. The sharp break in a local column accurately records what happened in that area through time. Acceptance of this point would release us from a self-imposed status of inferiority among the evolutionary sciences. The paleontologist's gut-reaction is to view almost any anomaly as an artifact imposed by our institutional millstone—an imperfect fossil record. But just as we now tend to view the

Problems of phyletic gradualism. In our alternate picture of phyletic gradualism, we are not confronted with a self-contained theory from modern biology. The postulated mechanism for gradual uni-directional change is "orthoselection," usually viewed as a constant adjustment to a uni-directional change in one or more features of the physical environment. The concept of orthoselection arose as an attempt to remove the explanation of gradual morphological change from the realm of metaphysics ("orthogenesis"). It does *not* emanate from *Drosophila* laboratories, but represents a hypothetical extrapolation of selective mechanisms observed by geneticists.

selection favoring intermediate rather than extreme phenotypes." In this view, the importance of peripheral isolates lies in their small size and the alien environment beyond the species border that they inhabit—for only here are selective pressures strong enough and the inertia of large numbers sufficiently reduced to produce the "genetic revolution" (Mayr, 1963, p. 533) that overcomes homeostasis. The coherence of a species, therefore, is not maintained by interaction among its members (gene flow). It emerges, rather, as an historical consequence of the species' origin as a peripherally isolated population that acquired its own powerful homeostatic system. (We regard this idea as a serious challenge to the conventional view of species' reality that depends upon the organization of species as ecological units of *interacting* individuals in nature. If groups of nearly-independent local populations are recognized as species only because they share a set of homeostatic mechanisms developed long ago in a peripheral isolate that was "real" in our conventional sense of interaction, then some persistent anomalies are resolved. The arrangement of must be retrospective. From this vantage point, it is very difficult to view evolution as anything but an easy and inevitable result of mere existence, as something that unfolds in a natural and orderly fashion. Yet we urge a different view. The norm for a species or, by extension, a community is stability. Speciation is a rare and difficult event that punctuates a system in homeostatic equilibrium. That so uncommon an event should have produced such a wondrous array of living and fossil forms can only give strength to an old idea: paleontology deals with a phenomenon that belongs to it alone among the evolutionary sciences and that enlightens all its conclusions—time.

GENETIC REVOLUTIONS, FOUNDER EFFECTS, AND SPECIATION

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INTRODUCTION

Are new species formed in rare catastrophes, distinct from the normal processes of phyletic evolution? Or does reproductive isolation evolve gradually, as a by-product of the divergence of gene pools? Mayr (120–124) has argued the former, holding that speciation usually results from genetic revolutions triggered by founder effects: An isolated population, small in numbers and in geographic extent, colonizes a new area. Both changes in selection pressures and genetic drift result in the rapid shift of many genes to a new, coadapted combination, which is reproductively isolated from the ancestral population. Carson (27, 29, 31) and Templeton (175–180), among others, have put forward similar models.

This cluster of theories is woven from many strands; we will try to tease these apart in order to find out precisely which processes may be involved in speciation by founder effect. By placing them in the context of other models, we will argue that, although founder effects may cause speciation under sufficiently stringent conditions, they are only one extreme of a continuous range of possibilities. Complete geographic isolation is unnecessary; absolute coadaptation between "closed" systems of alleles is unlikely; and divergence may be driven in a variety of ways, without the need for drastic external changes. Reproductive isolation is most likely to be built up gradually, in a

Evolution, 36(3), 1982, pp. 474–498

A NEO-DARWINIAN COMMENTARY ON MACROEVOLUTION

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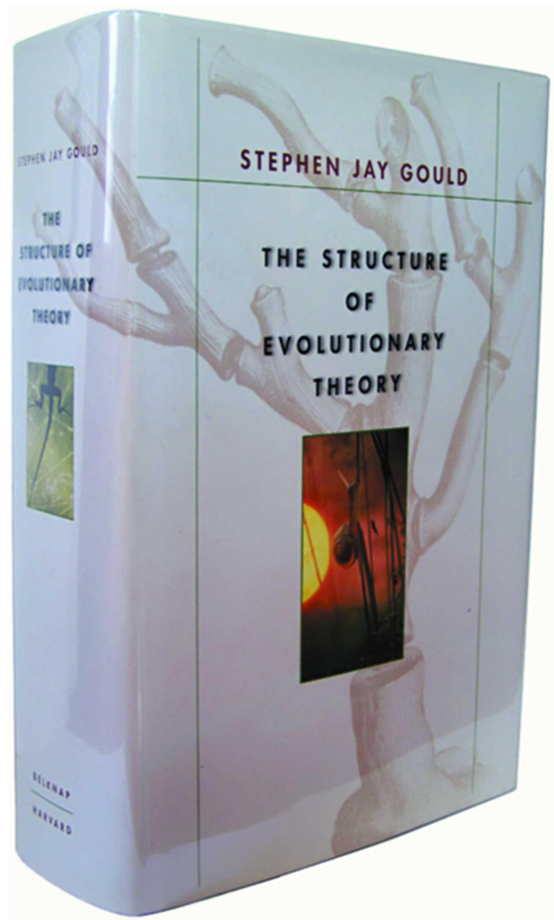
The neo-Darwinian synthesis that resulted from the integration of Mendelian genetics into evolutionary theory has dominated evolutionary biology for the last 30 to 40 years, due largely to its agreement with a huge body of experimental and observational data. The classic works representative of this school of thought come from the fields of genetics (Fisher, 1930; Wright, 1931; Haldane, 1932; Dobzhansky, 1937; Muller, 1940), development (de Beer, 1940), zoology, (Huxley, 1942; Mayr,

equilibria" theory of evolution (Eldredge and Gould, 1972; Gould, 1977, 1980; Stanley, 1975, 1979; Gould and Eldredge, 1977). Indeed, Gould (1980) states:

> "I have been watching it [neo-Darwinism] slowly unravel as a universal description of evolution . . . . I have been reluctant to admit it . . . but . . . that theory, as a general proposition, is effectively dead, despite its persistence as a text-book orthodoxy."

Gould's big book



Testable in the fossil record?

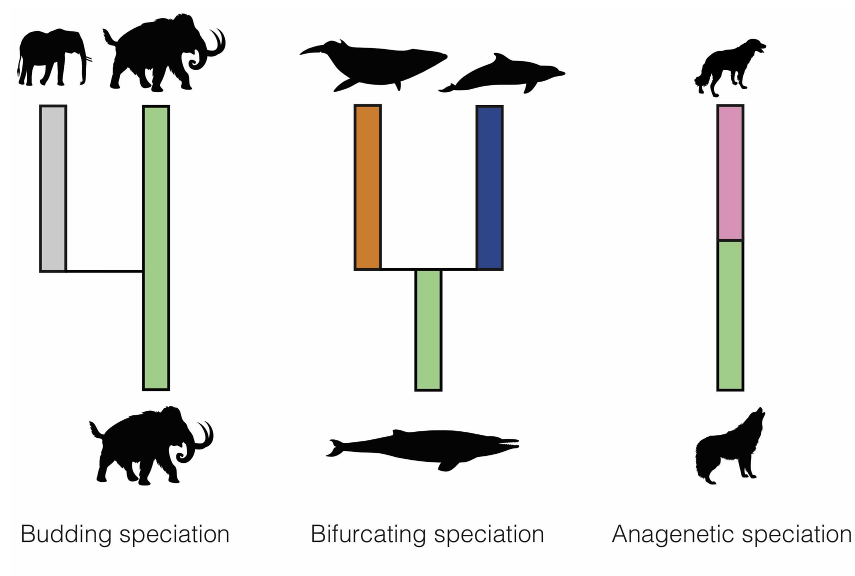
Morphospecies

Is speciation visible?

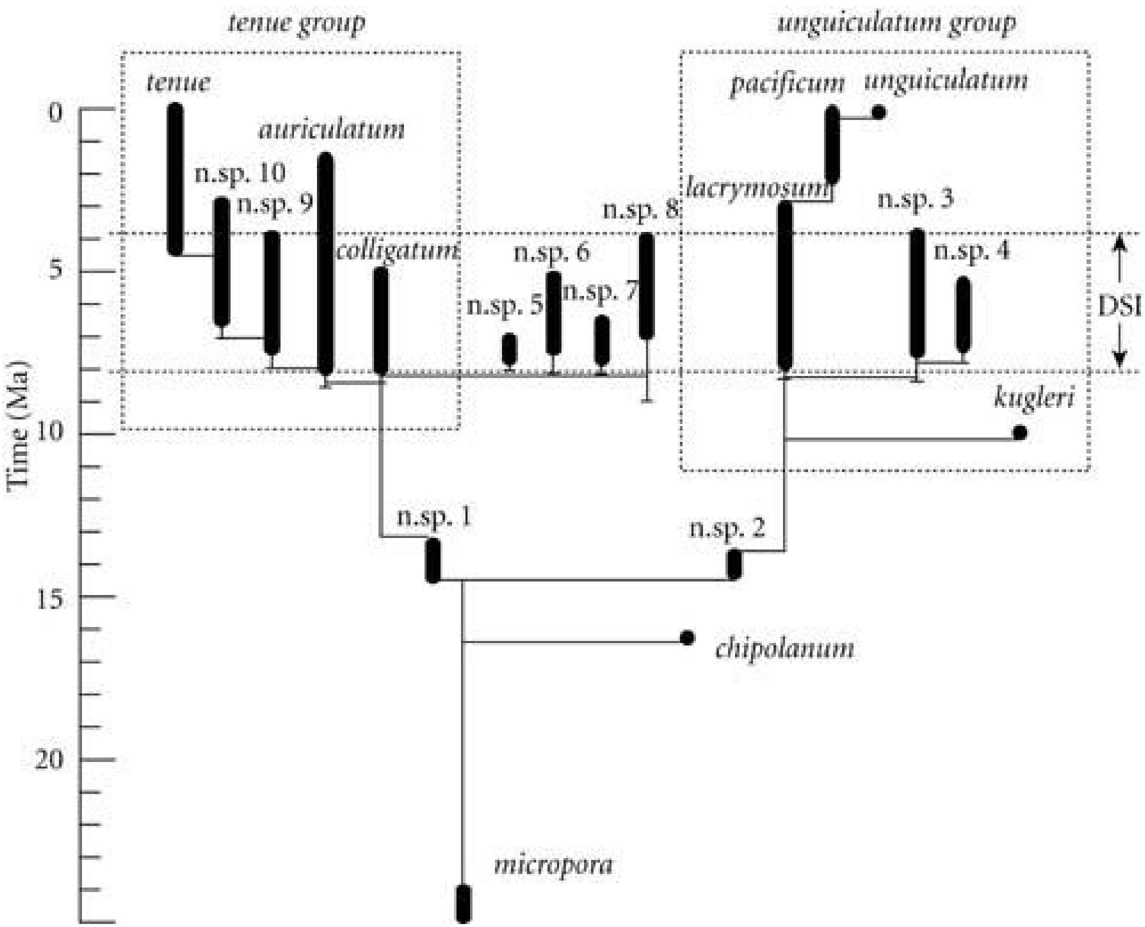
New modes for paleodata:

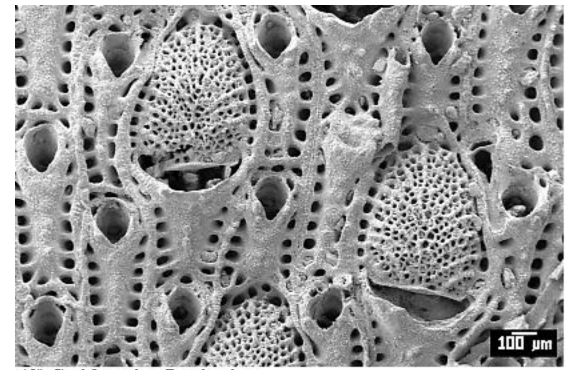
Budding speciation

Anagenetic speciation



Testable in the fossil record?





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Bryozoans:
Metrarabdatos

VOL. 195, NO. 5 THE AMERICAN NATURALIST MAY 2020

Revisiting a Landmark Study System: No Evidence for a Punctuated Mode of Evolution in *Metrarabdotos*

Kjetil Lysne Voje,[1,*] Emanuela Di Martino,[2] and Arthur Porto[1]

1. Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway; 2. Natural History Museum, University of Oslo, Blindern, PO Box 1172, Oslo 0318, Norway

Submitted March 18, 2019; Accepted November 14, 2019; Electronically published March 17, 2020

Online enhancements: supplemental PDF, 3D figure rotations. *Dryad data:* https://doi.org/10.5061/dryad.t4b8gthxm.

Problems with original analysis:

Not respecting scale (ordinal & nominal traits); differences meaningless in terms of magnitude

Replacing missing values with species means

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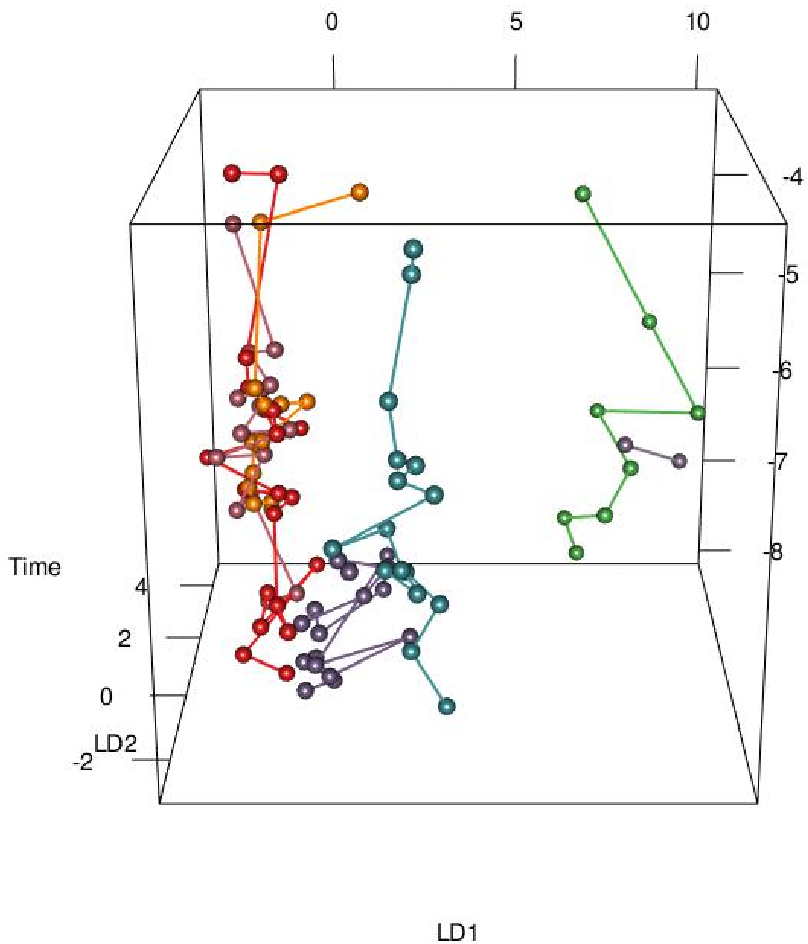
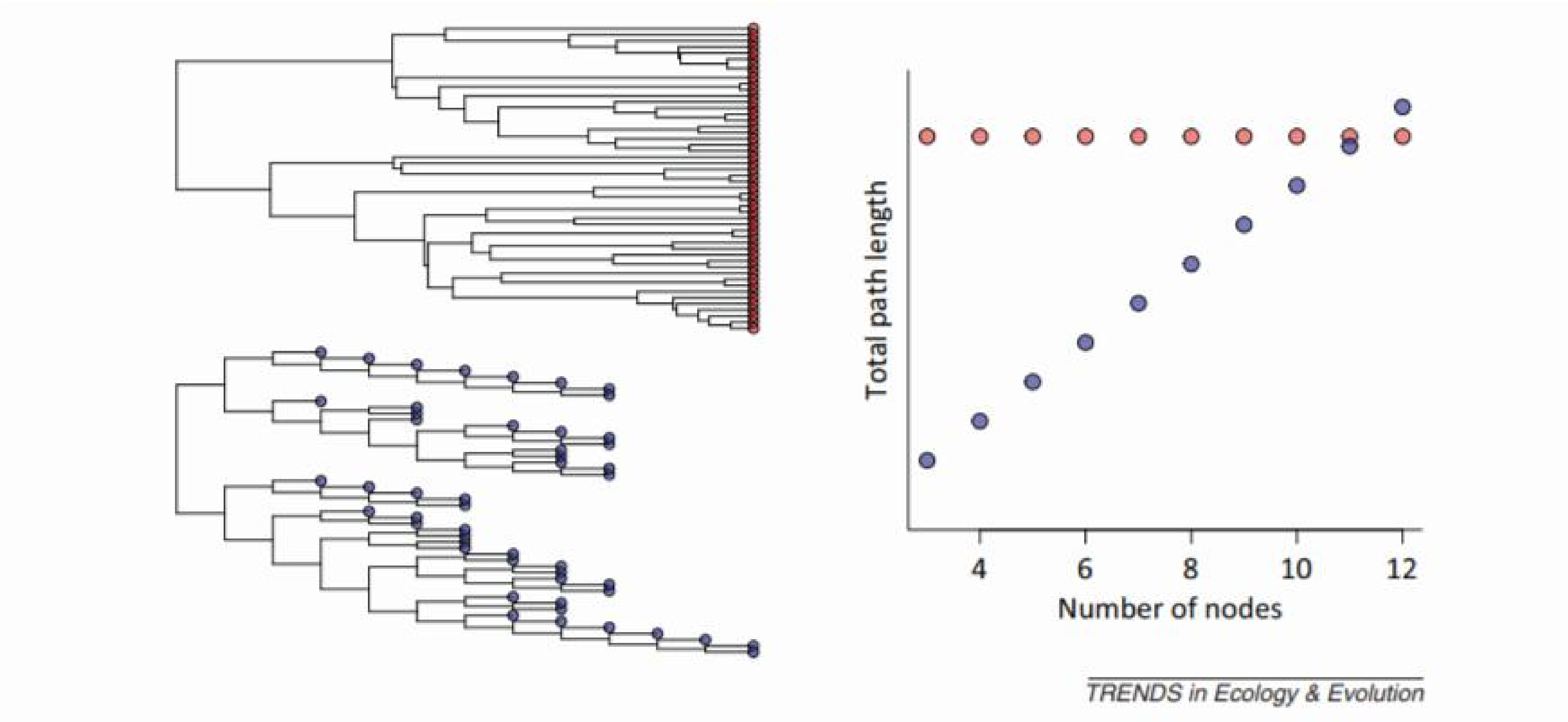


"We failed to find differences in evolutionary rates between anagenesis and cladogenesis in our reanalysis of a subset of the Metrarabdotos data. Separate lineages are not occupying distinct places in multivariate space but show large fluctuations that overlap extensively"

Testable with PCMs?



Our argument...

Review

Cell PRESS

Feature Review

Is there room for punctuated equilibrium in macroevolution?

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‘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’ ([1], p. 119].

‘This controversy, widely known as the ‘punctuated equilibrium’ debate, remained unresolved, largely owing to the difficulty of distinguishing biological species from fossil remains. We analyzed body masses of 2143 existing mammal species on a phylogeny comprising 4510 (i.e., nearly all) extant species to estimate rates of gradual (anagenetic) and speciational (cladogenetic) evolution’ ([2], p. 2195).

‘Under such processes, observations at the tips of a phylogenetic 40 tree have a multivariate Gaussian distribution, which may lead to suboptimal model specification under certain evolutionary conditions, as supposed in models of punctuated equilibrium or adaptive radiation’ ([3], p. 193).

Our argument...

“PE” is 4 distinct questions

1. What is the relative importance of gradualistic versus pulsed evolution?
2. What is the role of speciational events (cladogenesis) versus within lineage evolution (anagenesis) in generating trait divergence?
3. When change is cladogenetic, are these changes adaptive or driven by neutral processes?
4. How important is higher level selection (species selection) in shaping patterns of diversity?

Pulsed evolution is common

(gradual anagenetic change is too)

PNAS PNAS PNAS

Check for updates

Pulsed evolution shaped modern vertebrate body sizes

Michael J. Landis[a] and Joshua G. Schraiber[b,c,1]

[a]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520; [b]Department of Biology, Temple University, Philadelphia, PA 19122; and [c]Institute for Genomics and Evolutionary Medicine, Temple University, Philadelphia, PA 19122

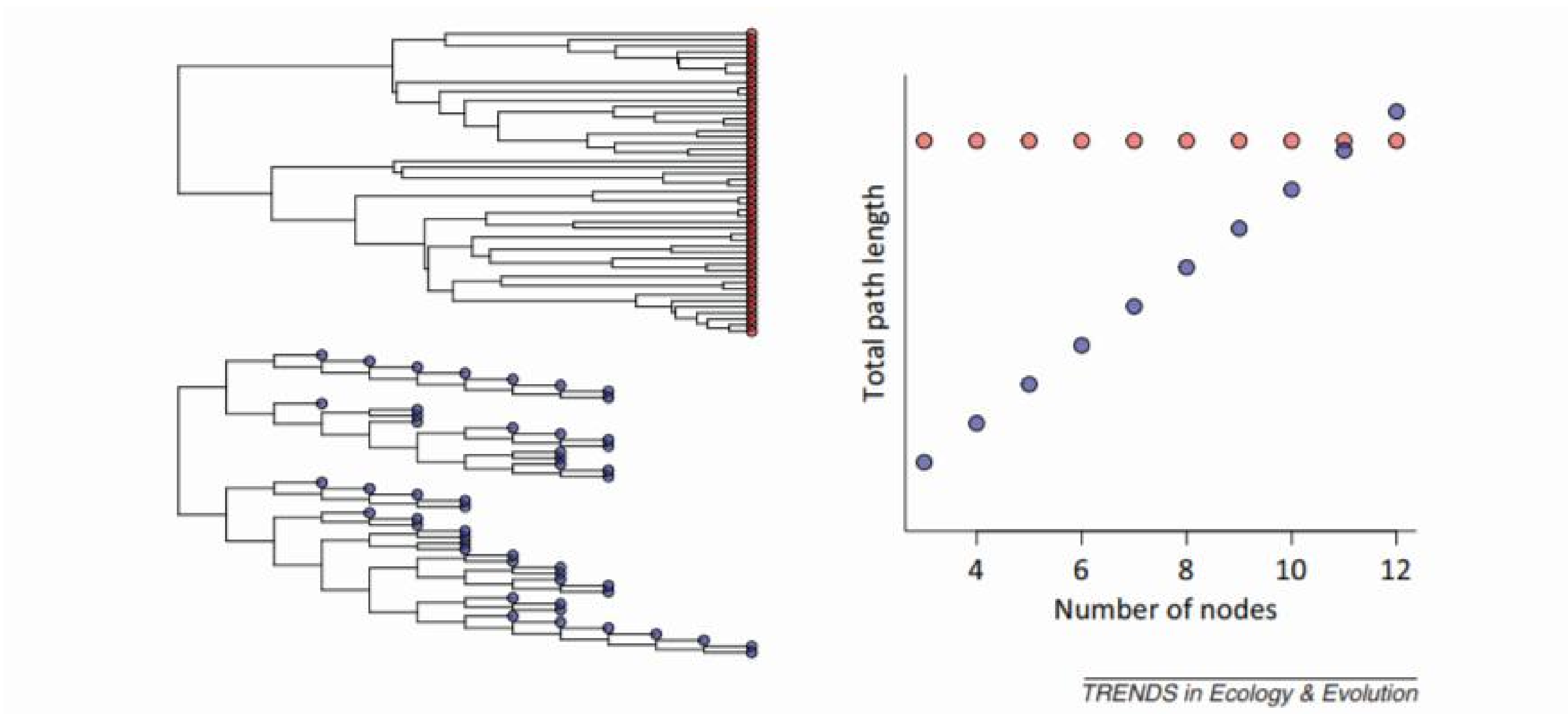
Edited by Neil H. Shubin, The University of Chicago, Chicago, IL, and approved October 6, 2017 (received for review June 18, 2017)

The relative importance of different modes of evolution in shaping phenotypic diversity remains a hotly debated question. Fossil data suggest that stasis may be a common mode of evolution, while modern data suggest some lineages experience very fast rates of evolution. One way to reconcile these observations is to imagine that evolution proceeds in pulses, rather than in increments, on geological timescales. To test this hypothesis, we developed a maximum-likelihood framework for fitting Lévy processes to comparative morphological data. This class of stochastic processes includes both an incremental and a pulsed component. We found that a plurality of modern vertebrate clades examined are best fitted by pulsed processes over models of incremental change, stationarity, and adaptive radiation. When we compare our results to theoretical expectations of the rate and speed of regime shifts for models that detail fitness landscape dynamics, we find that our quantitative results are broadly compatible with both microevolutionary models and observations from the fossil record.

ties of these methods, nor is much known about the prevalence of pulsed change throughout some of Earth's most intensely studied clades.

Here, we examine evidence for pulsed evolution across vertebrate taxa, using a method for fitting Lévy processes to comparative data. These processes can capture both incremental and pulsed modes of evolution in a single, simple framework. We apply this method to analyze 66 vertebrate clades containing 8,323 extant species for evidence of pulsed evolution by comparing the statistical fit of several varieties of Lévy jump processes (modeling different types of pulsed evolution) to three models that emphasize alternative macroevolutionary dynamics. Under these models, the adaptive optimum of a lineage may wander incrementally and freely (Brownian motion), it may change incrementally but remain stationary (Ornstein–Uhlenbeck), or it may change most rapidly following the initial diversification of a clade while decelerating over time, e.g., during an adaptive radi-

Speciation rates are correlated to trait change



Less clear if speciation is a significant cause of pulsed evolution; or an effect of another factor - still controversial

Does speciation cause adaptive radiation?

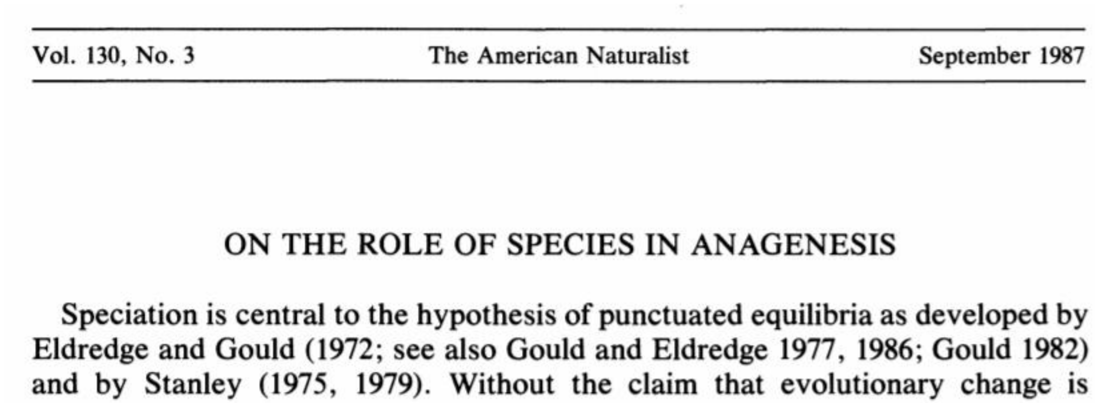
Does failure to speciate prevent some species from adapting?

The other side of the coin...Stasis

"Stasis is data"

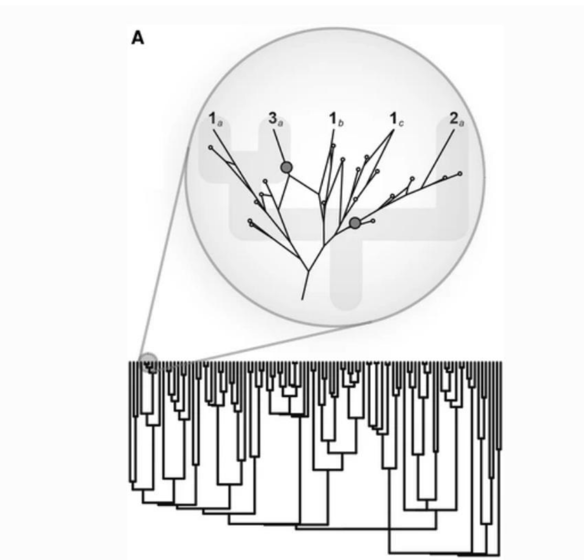
Microevolutionary theory can explain punctuations, but can it explain stasis?

Ephemeral divergence model

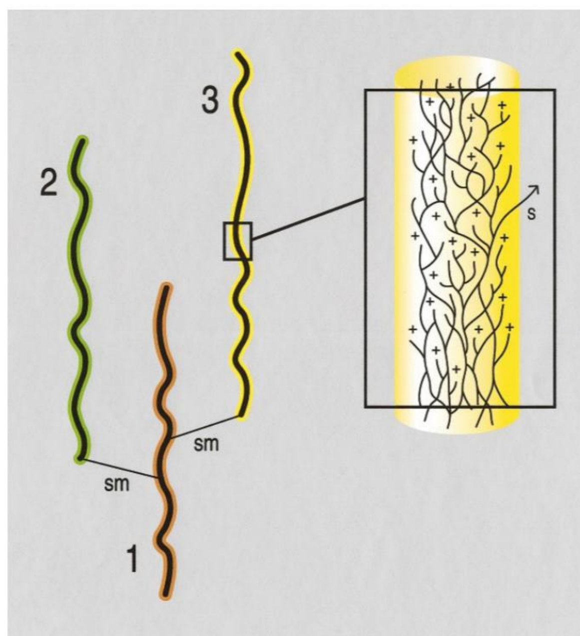

Vol. 130, No. 3 The American Naturalist September 1987

ON THE ROLE OF SPECIES IN ANAGENESIS

Speciation is central to the hypothesis of punctuated equilibria as developed by Eldredge and Gould (1972; see also Gould and Eldredge 1977, 1986; Gould 1982) and by Stanley (1975, 1979). Without the claim that evolutionary change is



related: Ephemeral speciation



Doug Futuyma

Rescued version of PE?

Here I point out a consequence of speciation that supports a highly qualified version of punctuated equilibrium. None of the ideas explored below is in itself original, but I am not aware that they have been explicitly developed in the present context. In brief, I propose that because the spatial locations of habitats shift in time, extinction of and interbreeding among local populations makes much of the geographic differentiation of populations ephemeral, whereas reproductive isolation confers sufficient permanence on morphological changes for them to be discerned in the fossil record. Long-term anagenetic change in some characters is then the consequence of a succession of speciation events. I have briefly referred to this argument before (Futuyma 1986*a*, pp. 404, 406; Futuyma 1986*b*, p. 377), without having developed the reasoning, evidence, and contrasts with alternative hypotheses presented here.