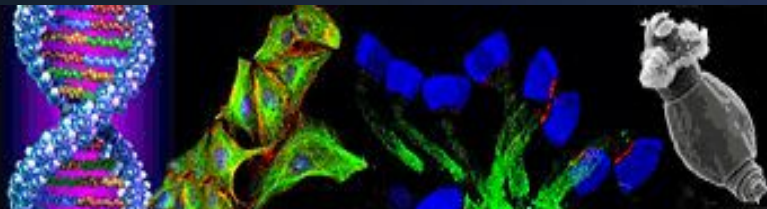


Gli equilibri punteggiati messi alla prova

Marco Ferraguti

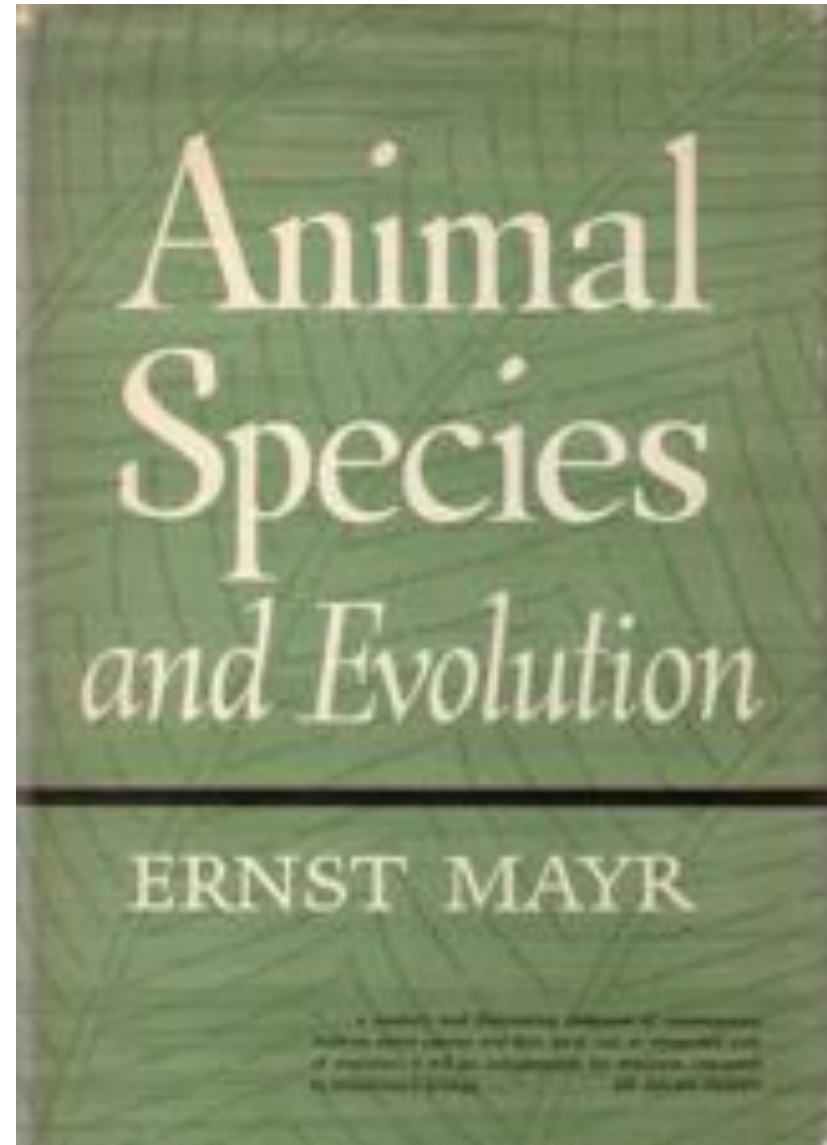
**Dipartimento di
BIOSCIENZE**

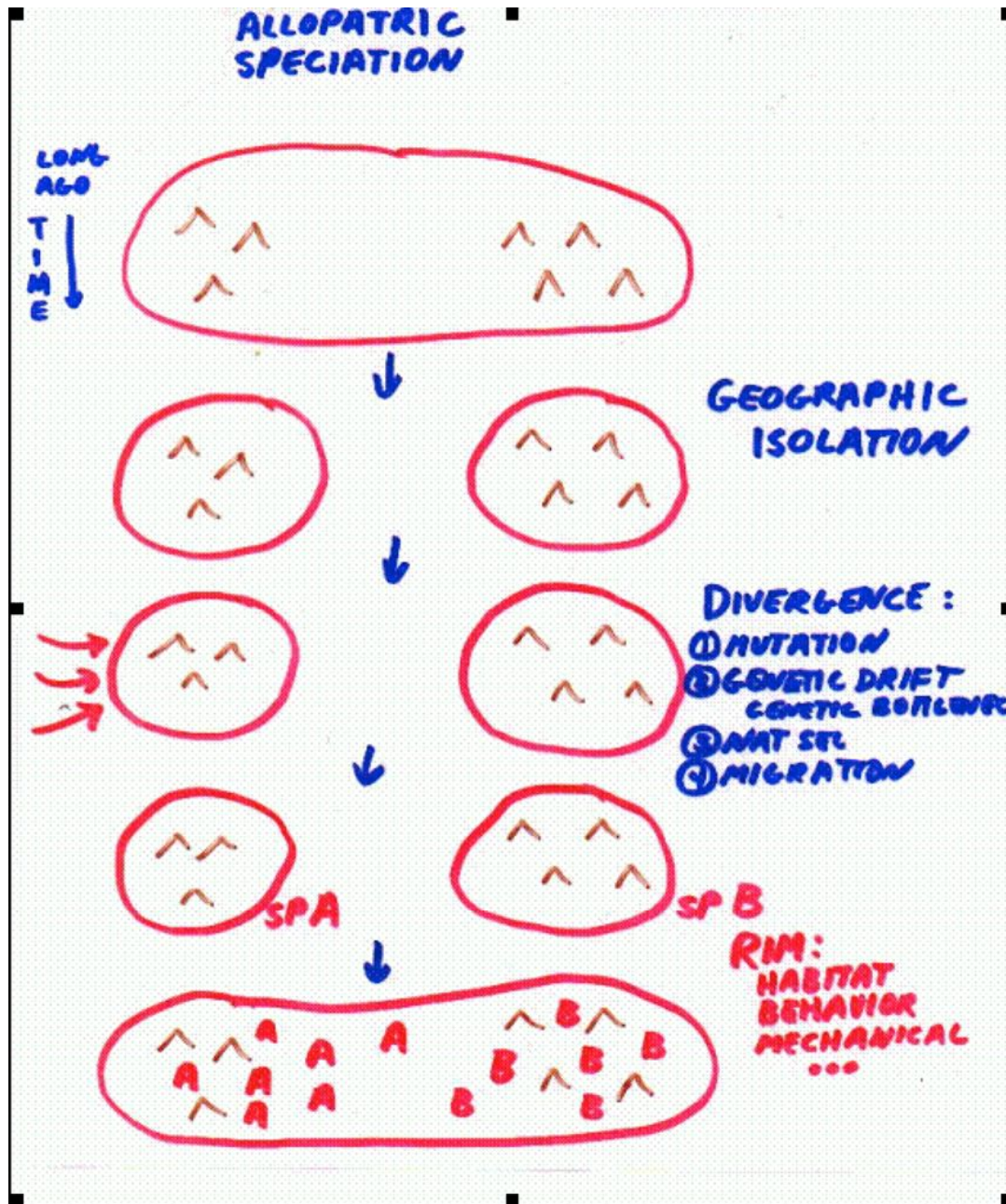


**UNIVERSITÀ
DEGLI STUDI
DI MILANO**

1. **Le radici profonde degli equilibri punteggiati**
2. **Il modello**
3. **Le reazioni della comunità degli evolucionisti**
4. **Le «prove»**

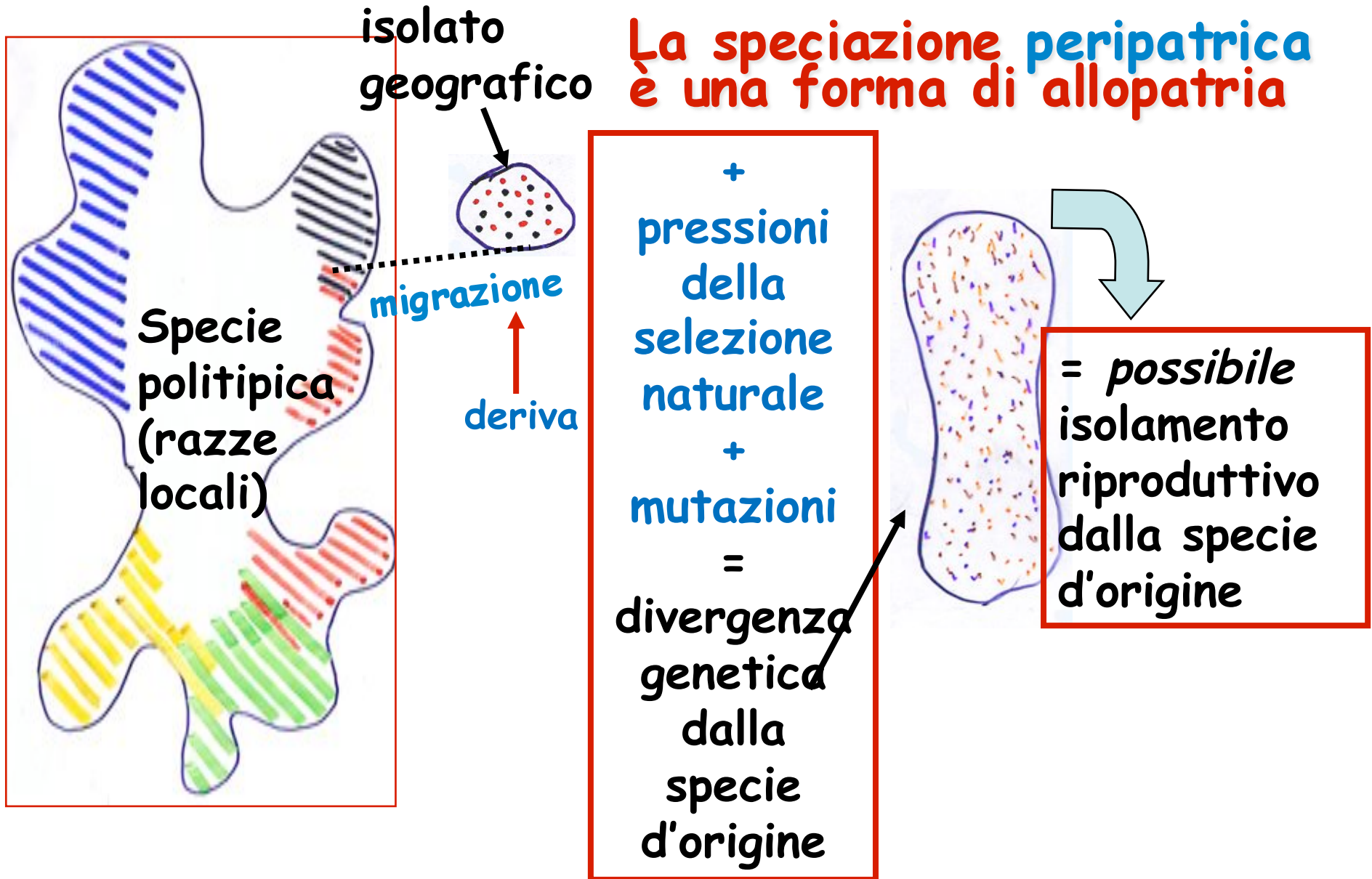
Ernst Mayr (1904-2005)



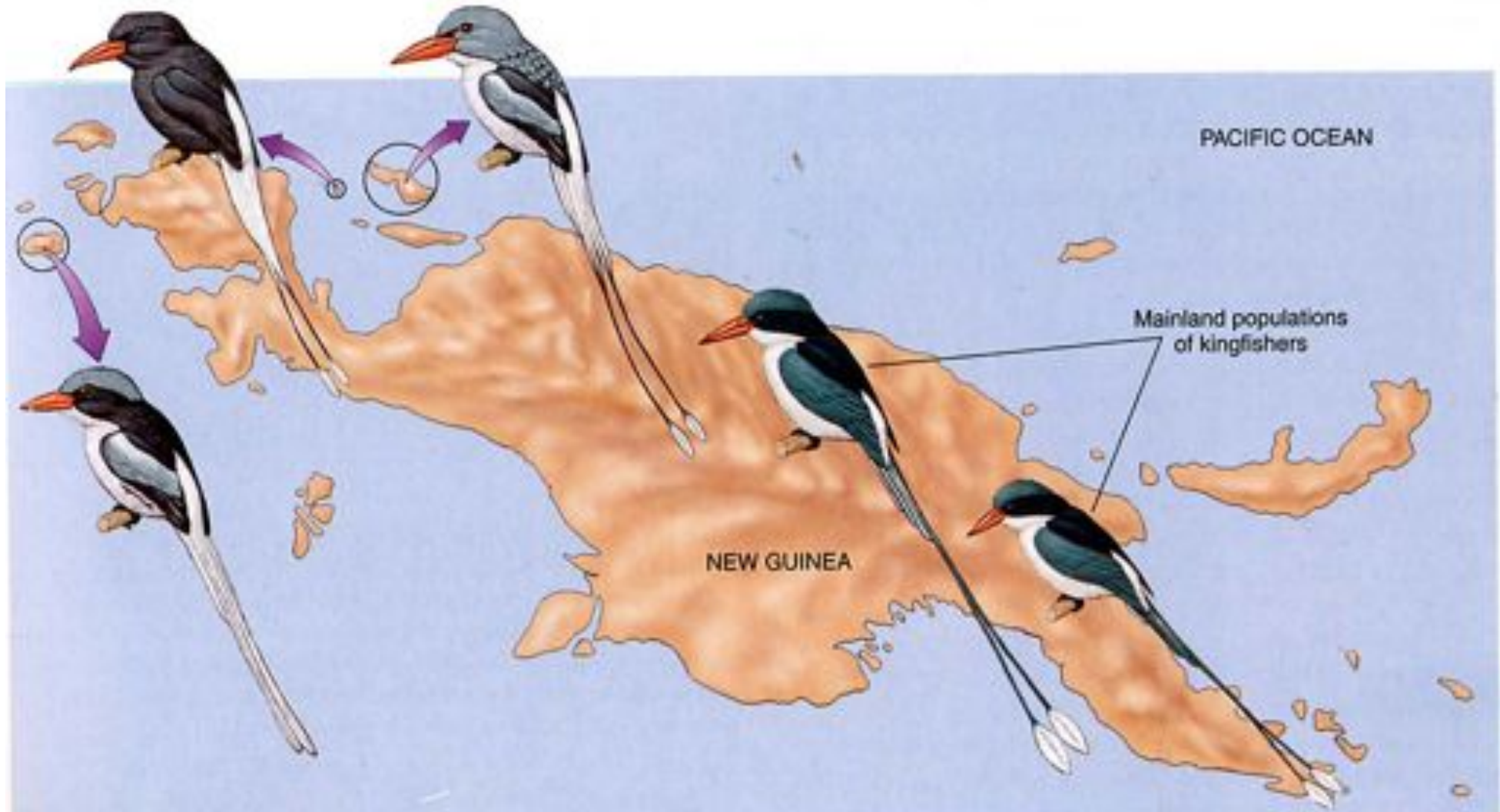


Il modello classico della speciazione allopatrica

La speciazione peripatrica è una forma di allopatria



Le popolazioni "di terraferma" del martin pescatore *Tanysiptera* in Nuova Guinea sono uniformi, mentre le popolazioni delle isolette circostanti sono differenziate "come fossero" specie diverse



the peripheral isolates model (PIM) (=peripatric *sensu* Mayr, 1963), has been regarded as the dominant mode of animal speciation

(Frey, *Syst Biol.*, 42, 373, 1993)

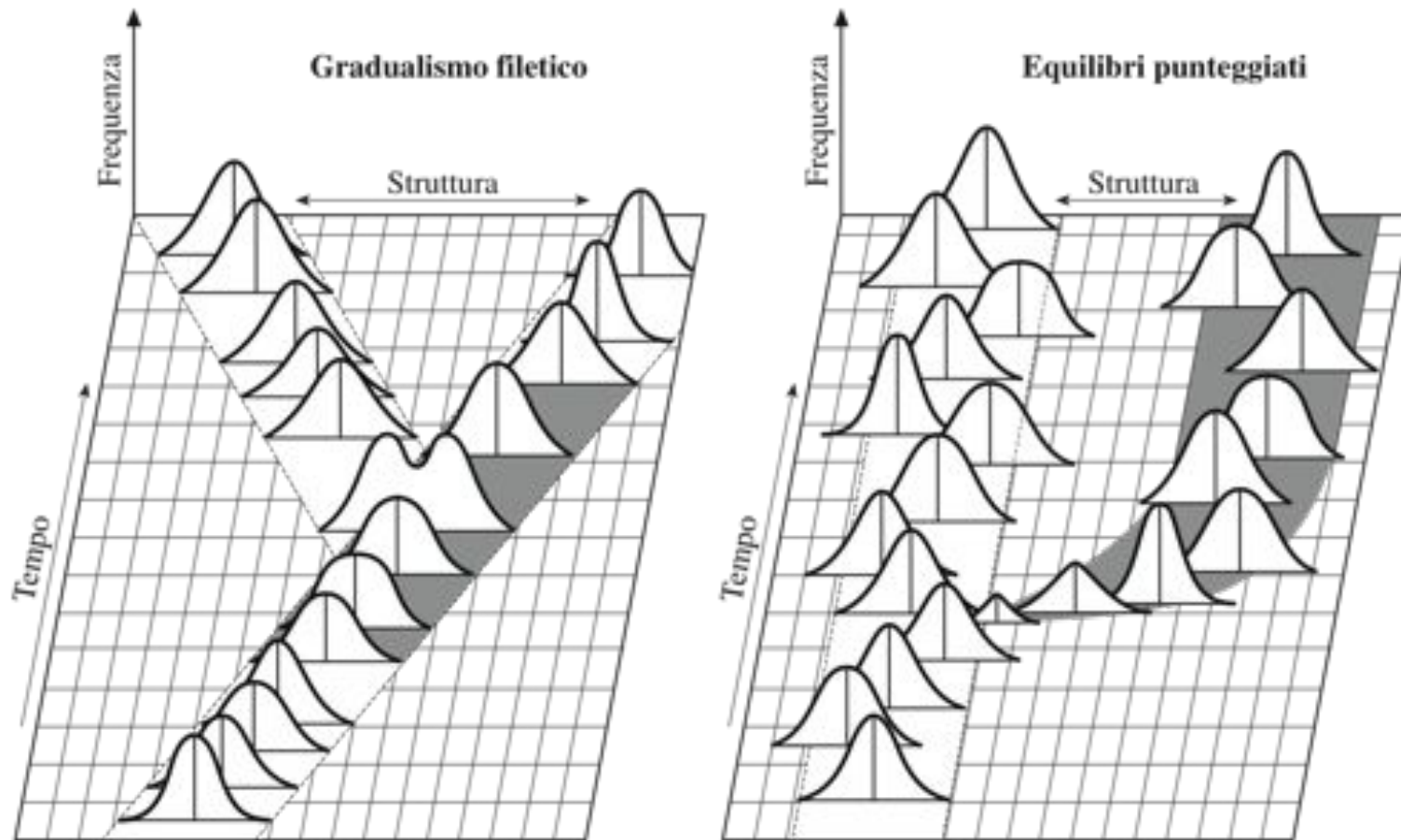


Che resti fossili dobbiamo attenderci, se le speciazioni avvengono prevalentemente in modo peripatrico?



Speciazione e variazioni nel tempo degli areali di tre specie successive ipotetiche, **A**, **B** e **C**

1. Le radici profonde degli equilibri punteggiati
2. Il modello
3. Le reazioni della comunità degli evolucionisti
4. Le «prove»



“La storia della vita è più adeguatamente rappresentata dal quadro degli “equilibri punteggiati” che dalla nozione del gradualismo filetico. La storia dell’evoluzione non è un grandioso dispiegamento, ma una sequenza di equilibri omeostatici, disturbati solo “raramente” (cioè abbastanza spesso nella pienezza dei tempi) da rapidi ed episodici eventi di speciazione” (Eldredge & Gould, 1972)

1. **Le radici profonde degli equilibri punteggiati**
2. **Il modello**
3. **Le reazioni della comunità degli evoluzionisti**
4. **Le «prove»**

Punctuated Equilibria—Where is the Evidence?

PHILIP D. GINGERICH

Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109

mon element of gradualism. Stasis can be viewed, in this instance, as gradualism at zero rate. Further, punctuated equilibria as an alternative to gradualism is not supported by gaps in the fossil record: gaps are gaps, providing no evidence of transition. Without positive empirical evidence, punctuated equilibria, like saltation, cannot be sustained as an alternative to gradualism. Perhaps the time has come to end this false debate and concentrate instead on study of the rates and patterns we can observe.

Curiosamente anche Mayr si associa...

C'è un particolare aspetto che differenzia in modo fondamentale Gould e Eldredge da Mayr: essi affermano che gli equilibri intermittenti sono prodotti da discontinuità di dimensioni tali da corrispondere ai mostri di belle speranze di Goldschmidt: «La macroevoluzione avanza grazie al raro successo di tali mostri di belle speranze, e non mediante continui piccoli cambiamenti all'interno delle popolazioni» (Gould, 1977b, p. 30). Ciò che Goldschmidt aveva ipotizzato, e che Gould sembra sottoscrivere, è la produzione di nuove specie o di taxa superiori in un'unica tappa mediante un singolo individuo. Mayr, al contrario, considera l'evoluzione nelle popolazioni fon-

1. Le radici profonde degli equilibri punteggiati
2. Il modello
3. Le reazioni della comunità degli evolucionisti
4. Le «prove»

Animal Species *and Evolution*

ERNST MAYR

A lucidly and thoroughly detailed account of evolutionary biology that places and clarifies the central role of species in all biological systems. An essential volume for students and scholars alike. —*Booklist*

Parliamo di percentuali!

E' difficile mettere un numero sotto a "basso" e "predominante". Una affermazione a spanne del 90 % è sufficiente a scagionarmi dall'accusa di costruirmi una vittoria facile? Se Dio apparisse e ci informasse che il 48.647 % degli eventi evolutivi importanti è avvenuto per equilibri punteggiati, io ne sarei più (poco più) che semisoddisfatto. Avere mezza ragione, tuttavia, è una benedizione in un mondo complesso.

S.J.Gould *Scientia*, 1983, 118, 135, 1983

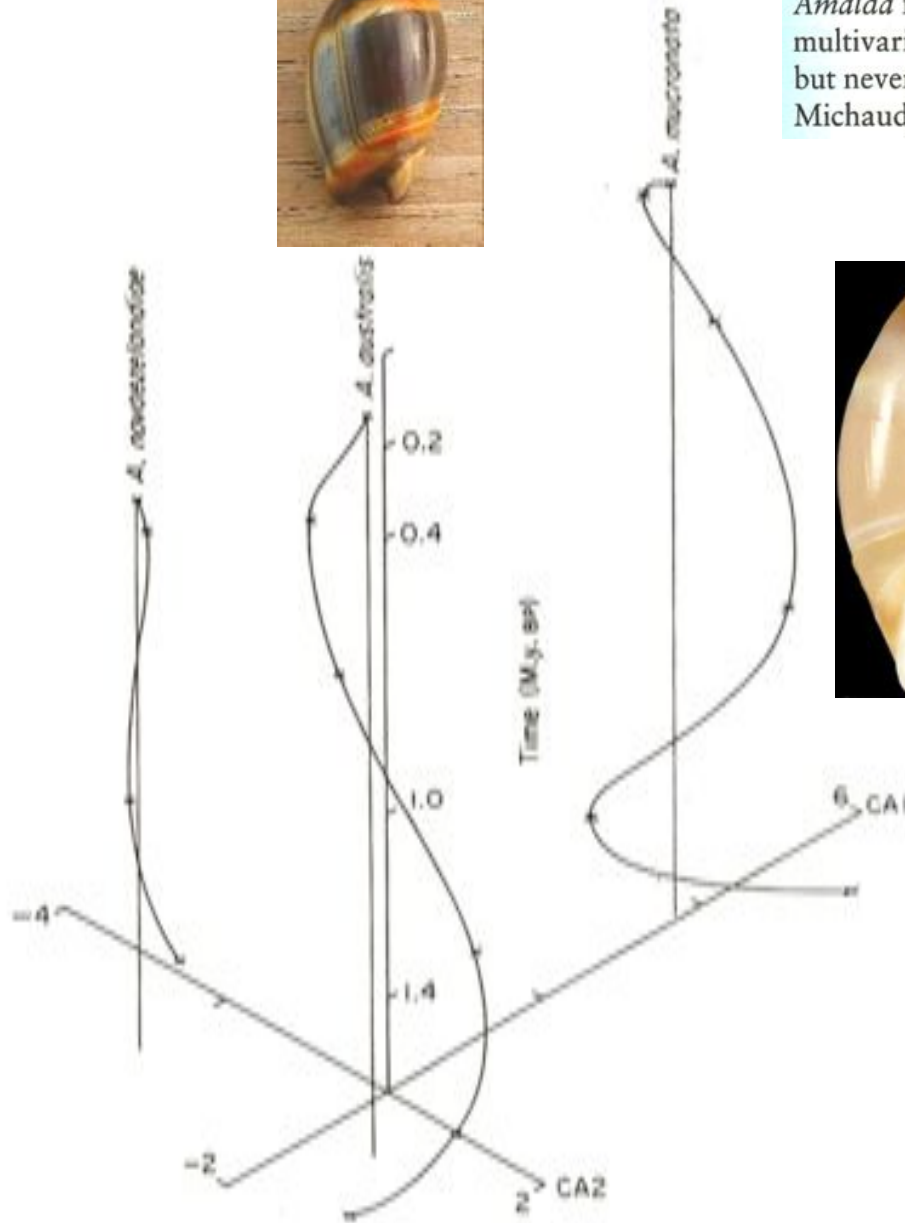
In una rassegna su 48 studi esaminati di le frequenze sono:

- ▶ 31 % gradualismo
- ▶ 21% gradualismo + stasi
- ▶ 48% punteggiature + stasi

Erwin & Anstey *New approaches to speciation in the fossil record*, CUP, 1995



9-8. Stasis in three genetically well defined extant species of the gastropod *Amalda* from New Zealand, based on 662 fossil specimens. Mean values in multivariate expression based on all ten variables fluctuate mildly through time but never depart from the range of variation within extant populations. From Michaud, 1989.



**La stasi esiste,
ecco!**

Paleobiology, 31(2), 2005, pp. 133–145

The dynamics of evolutionary stasis

Niles Eldredge, John N. Thompson, Paul M. Brakefield, Sergey Gavrilets, David Jablonski, Jeremy B. C. Jackson, Richard E. Lenski, Bruce S. Lieberman, Mark A. McPeck, and William Miller III

«Che cosa, dunque, limita la diffusione del cambiamento evolutivo, quando dati sperimentali e di campo mostrano chiaramente che il potenziale per un cambiamento rapido è quasi sempre presente all'interno delle popolazioni?»

The million-year wait for macroevolutionary bursts

Josef C. Uyeda^{a,1}, Thomas F. Hansen^b, Stevan J. Arnold^a, and Jason Pienaar^c

^aDepartment of Zoology, Oregon State University, Corvallis, OR 97331; ^bDepartment of Biology, Centre for Ecological and Evolutionary Synthesis, University of Oslo, 0316 Oslo, Norway; and ^cDepartment of Genetics, University of Pretoria, Pretoria, South Africa 0002

Edited by Mark A. McPeck, Dartmouth College, Hanover, NH, and accepted by the Editorial Board July 22, 2011 (received for review October 11, 2010)

We lack a comprehensive understanding of evolutionary pattern and process because short-term and long-term data have rarely been combined into a single analytical framework. Here we test alternative models of phenotypic evolution using a dataset of unprecedented size and temporal span (over 8,000 data points). The data are body-size measurements taken from historical

studies, represent large datasets, and evolution reveal a pattern across taxa that often occurs over constrained intervals. We find that a pattern of

substantial bursts of phenotypic change with bounded fluctuations on shorter timescales. We suggest that these rare bursts reflect permanent changes in adaptive zones, whereas the short-term fluctuations represent local variations in niche optima due to restricted environmental variation within a stable adaptive zone.

Database. We compiled datasets that measure evolutionary divergence in size-related traits from three types of data: (i) contemporary field and historical studies, (ii) fossil time series, and (iii) phylogenetic comparative data. For the first two categories, we have drawn from the original databases of Gingerich (7) and Hendry et al. (8), which also include the entirety of the size-related data used in Estes and Arnold (21). We also added 29 additional

contemporary field and historical studies, (ii) fossil time series, and (iii) phylogenetic comparative data. For the first two categories, we have drawn from the original databases of Gingerich (7) and Hendry et al. (8), which also include the entirety of the size-related data used in Estes and Arnold (21). We also added 29 additional datasets (SI Text and Fig. S1) that include data by using branch lengths that includes 6,053 evolutionary and divergence estimates over the span of the last 57 Myr) by combining historical and contemporary field studies, fossil time series, and comparative data.

Results and Discussion

Consistent with previous studies (21, 22) we find a complete absence of a time-span effect up to ~ 1 Myr, but this pattern then

misure corporee prese dai più diversi esempi di cambiamento in fossili e popolazioni attuali: 6053 misure di divergenza morfometrica da 169 studi microevolutivi e paleontologici di uccelli, mammiferi e squamati

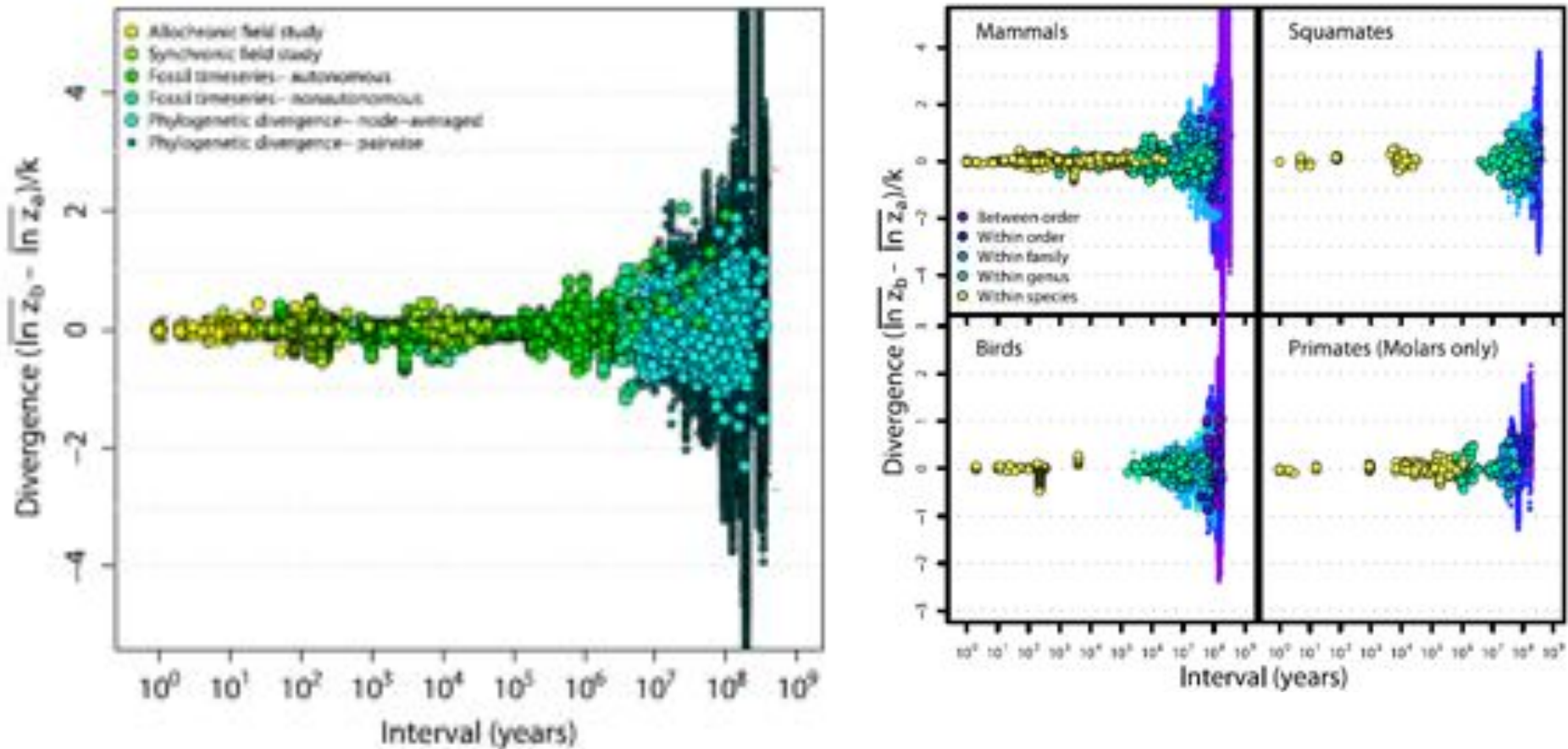


Fig. 1. The “blunderbuss pattern”, showing the relationship between evolutionary divergence and elapsed

Evoluzioni rapide a breve termine avvengono spesso in intervalli più brevi di un milione di anni, ma non si accumulano nel tempo; a tempi più lunghi (1-360 myr) vi è comunque un aumento di divergenza nel tempo.

Il modello migliore per spiegare i dati è quello che combina rari ma sostanziali «esplosioni» di cambiamento fenotipico con fluttuazioni limitate a tempi brevi

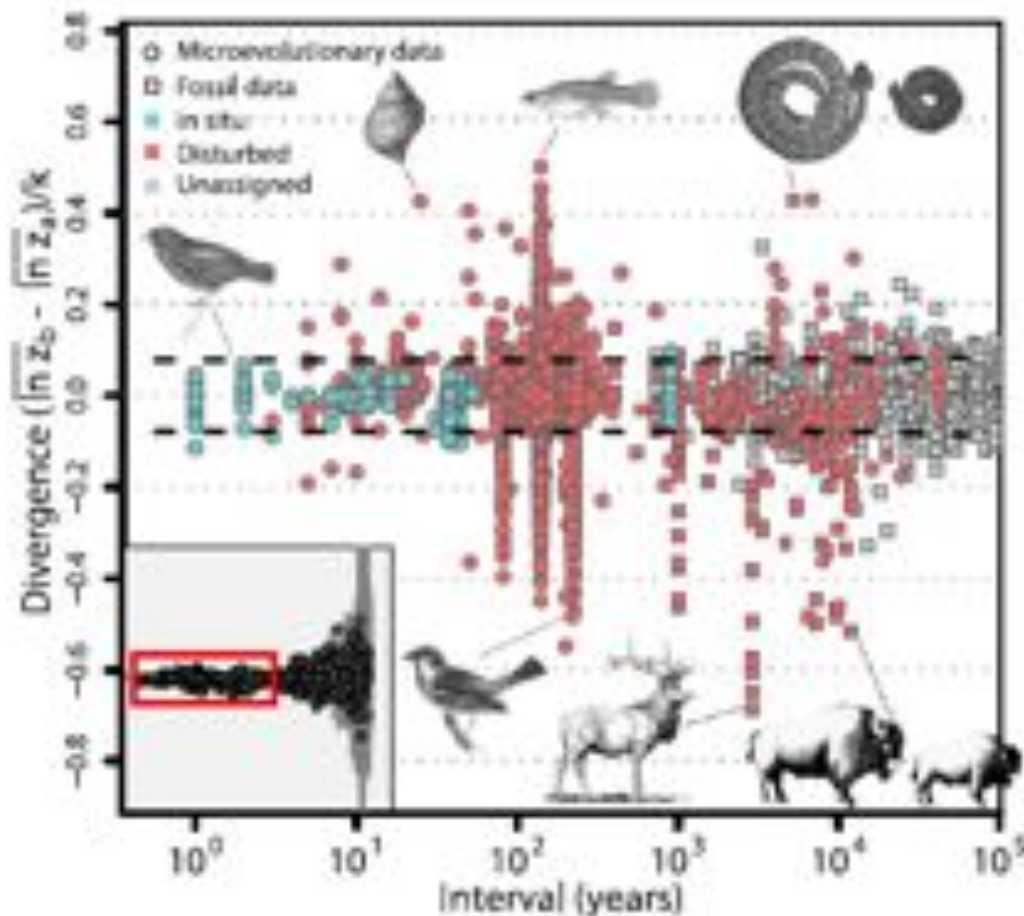


Fig. 5. Divergence identifiable as natural in situ variation vs. disturbance mediated community change demonstrates that the majority of cases of rapid evolution over microevolutionary timescales are from identifiable causes such as introductions, anthropogenic disturbances, and island isolation. Highlighted examples include (clockwise, starting from left) in situ evolution of *Geospiza fortis* in response to natural climate variation, divergence in *Nucella lapillus* in response to an introduced predator,

Introduction of *Gambusia affinis* to Nevada and Hawaii, island–mainland divergence in *Crotalus mitchelli*, Holocene dwarfing of *Bison antiquus* to *B. bison*, dwarfing of *Cervus elaphus* on Jersey Island, and the introduction of *Passer domesticus* to North America and New Zealand. Dotted lines indicate the 95% confidence interval

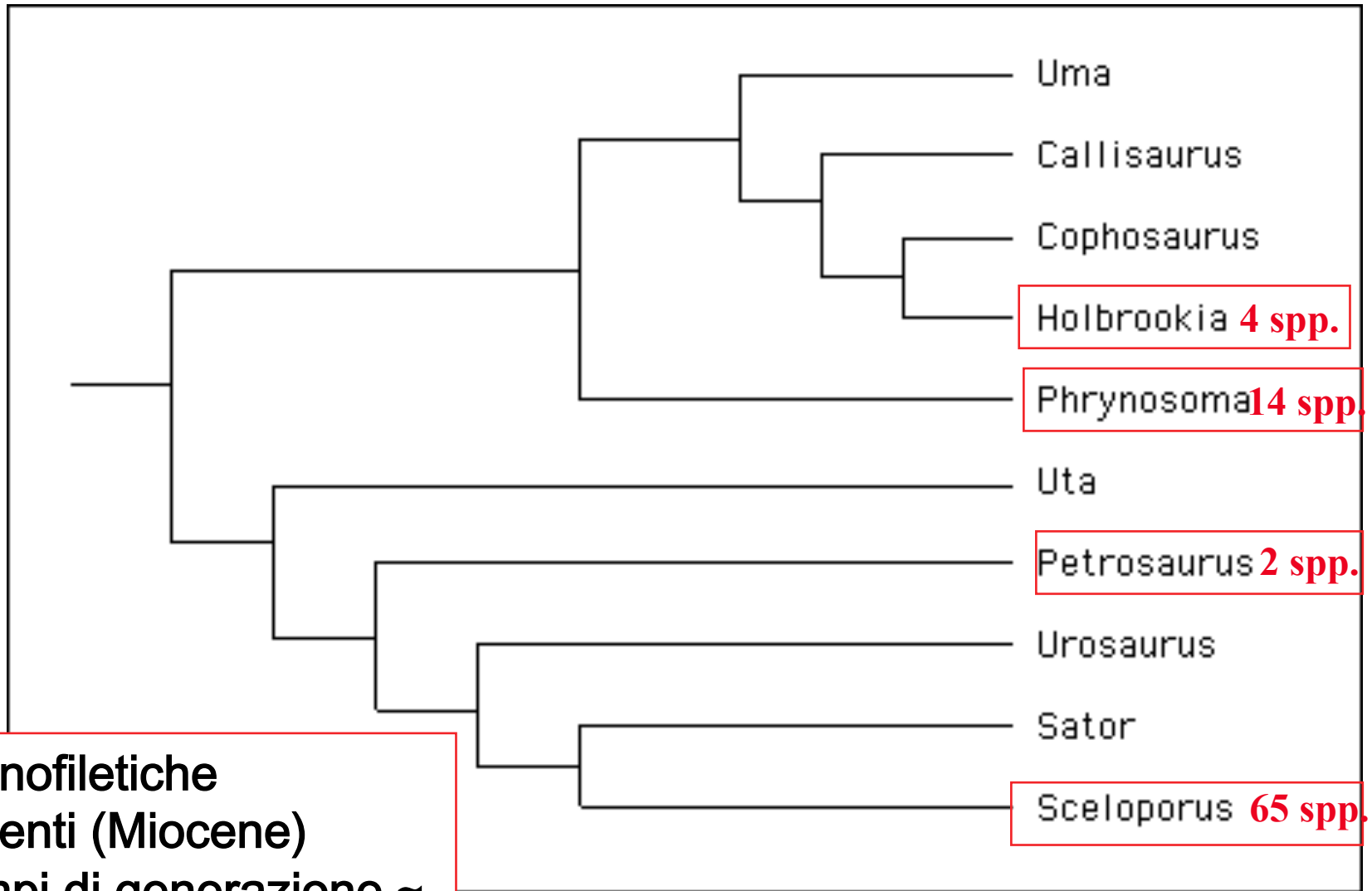
J. Evol. Biol. 3: 125-131 (1990)

D.P. Mindell, J. W. Sites Jr, & D. Graur

Mode of allozyme evolution: Increased genetic distance associated with speciation events

Se è vero il gradualismo filetico, le distanze genetiche sono strettamente funzione del tempo, e saranno le medesime in cladi ricchi o poveri di specie, purché di pari età. Per converso, se il tasso di evoluzione aumenta durante le speciazioni, e dunque prevalgono gli equilibri punteggiati, le distanze genetiche dovrebbero essere più elevate nei cladi ricchi di specie, con la maggiore divergenza genetica che deriva dal più elevato numero di eventi di speciazione nei cladi più speciosi.

filogenesi delle lucertole sceloporine



- monofiletiche
- recenti (Miocene)
- tempi di generazione \cong
- habitat simili, desertici
- simili tassi di estinzione

distanza genetica media fra 2 specie scelte a caso in un genere

tempo

Numero di eventi di speciazione

$$D = tD_a + nD_c$$

Divergenza causata da "gradualismo" per anno

Divergenza causata da ogni evento di speciazione

Purché: D_a sia costante
 gli eventi di speciazione contribuiscano ugualmente

Table 2. Species diversity, mean genetic distance (D), D_s/D_p ratios, and mean number of speciation events (S) separating two species belonging to a sceloporine lizard genus.

Genus	No. of species in genus	No. of species compared	No. of loci resolved	D	D_s/D_p	S
<i>Sceloporus</i>	65	28	26	0.877	—	22.97
<i>Phrynosoma</i>	14	4	25	0.512	1.713	5.86
<i>Holbrookia</i>	4	3	25	0.373	2.351	2.16
<i>Crotaphytus</i>	3	3	25	0.312	2.811	1.67
<i>Petrosaurus</i>	2	2	34	0.118	7.432	1.00

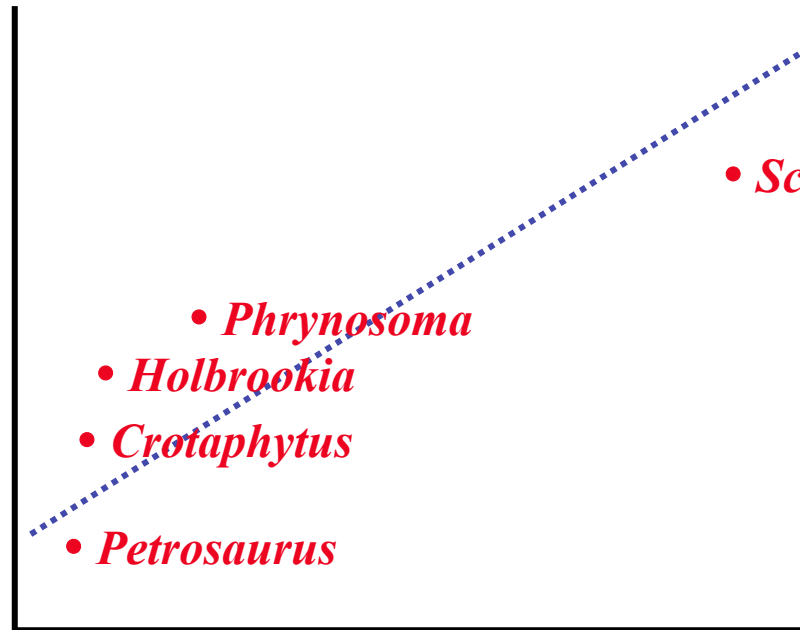


Phrynosoma



Holbrookia

$$D = tD_a + nD_c$$

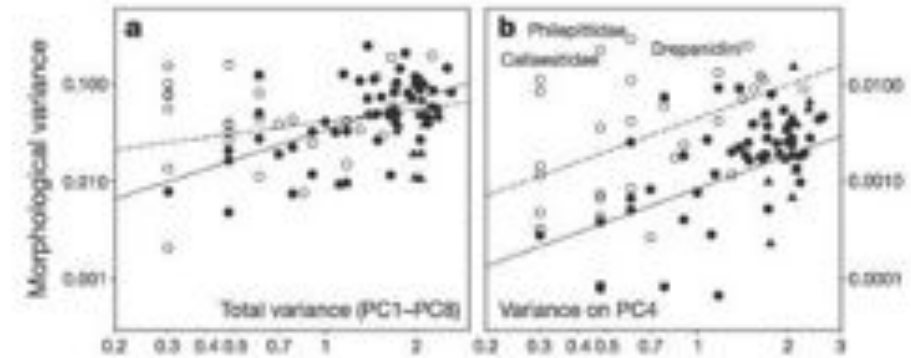


speciosità

Cladogenesis and morphological diversification in passerine birds

Robert E. Ricklefs

“The results show clearly that number



Confronta la **morfologia di 1018 (il 17,8%)
specie di passeriformi**

I risultati mostrano chiaramente che il numero di specie esercita una forte influenza sulla varianza morfologica indipendente dal tempo

Dunque, l'evoluzione morfologica negli uccelli sembra essere associata con la cladogenesi

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

Mark Pagel,* Chris Venditti, Andrew Meade

- analizzate 122 gruppi di sequenze geniche **pubblicate** di taxa di animali, piante e funghi

- Costruiti gli alberi filogenetici

- Costruita la lunghezza del cammino $X = n\beta + g$

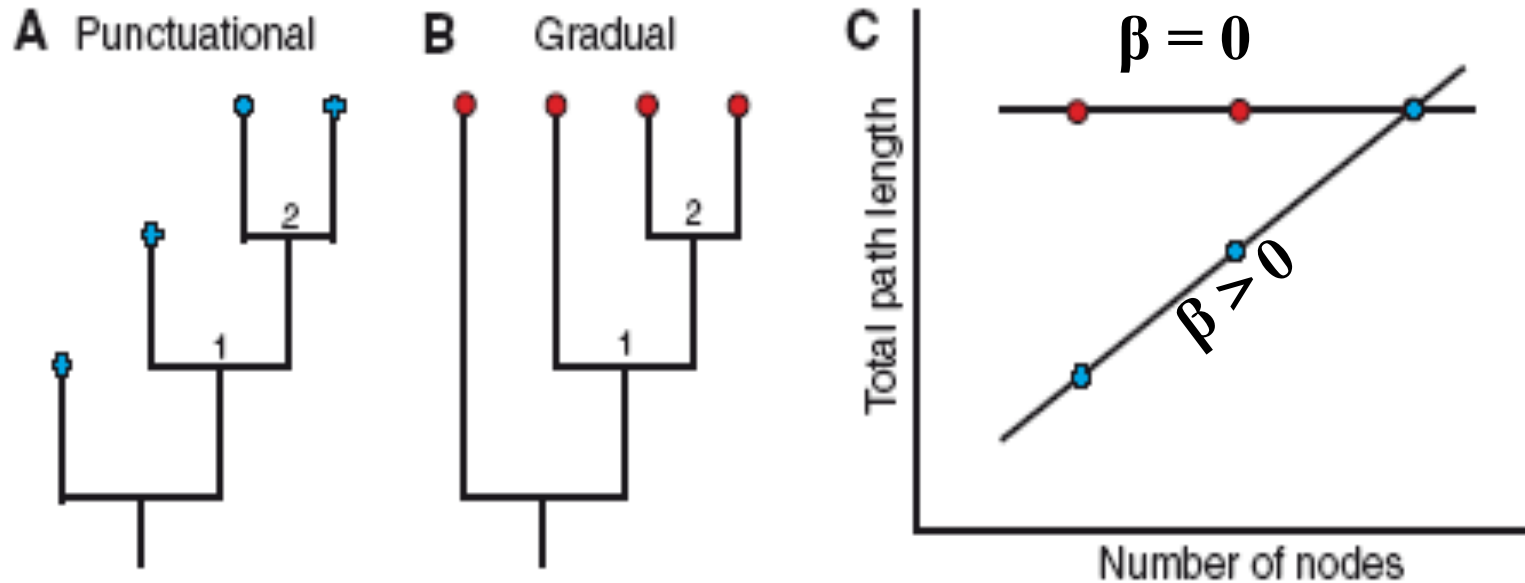
dove n è il numero dei nodi dell'albero

β è il contributo della speciazione all'evoluzione

g è il contributo dell'evoluzione graduale

(entrambi misurati in sostituzioni nucleotidiche attese per sito)

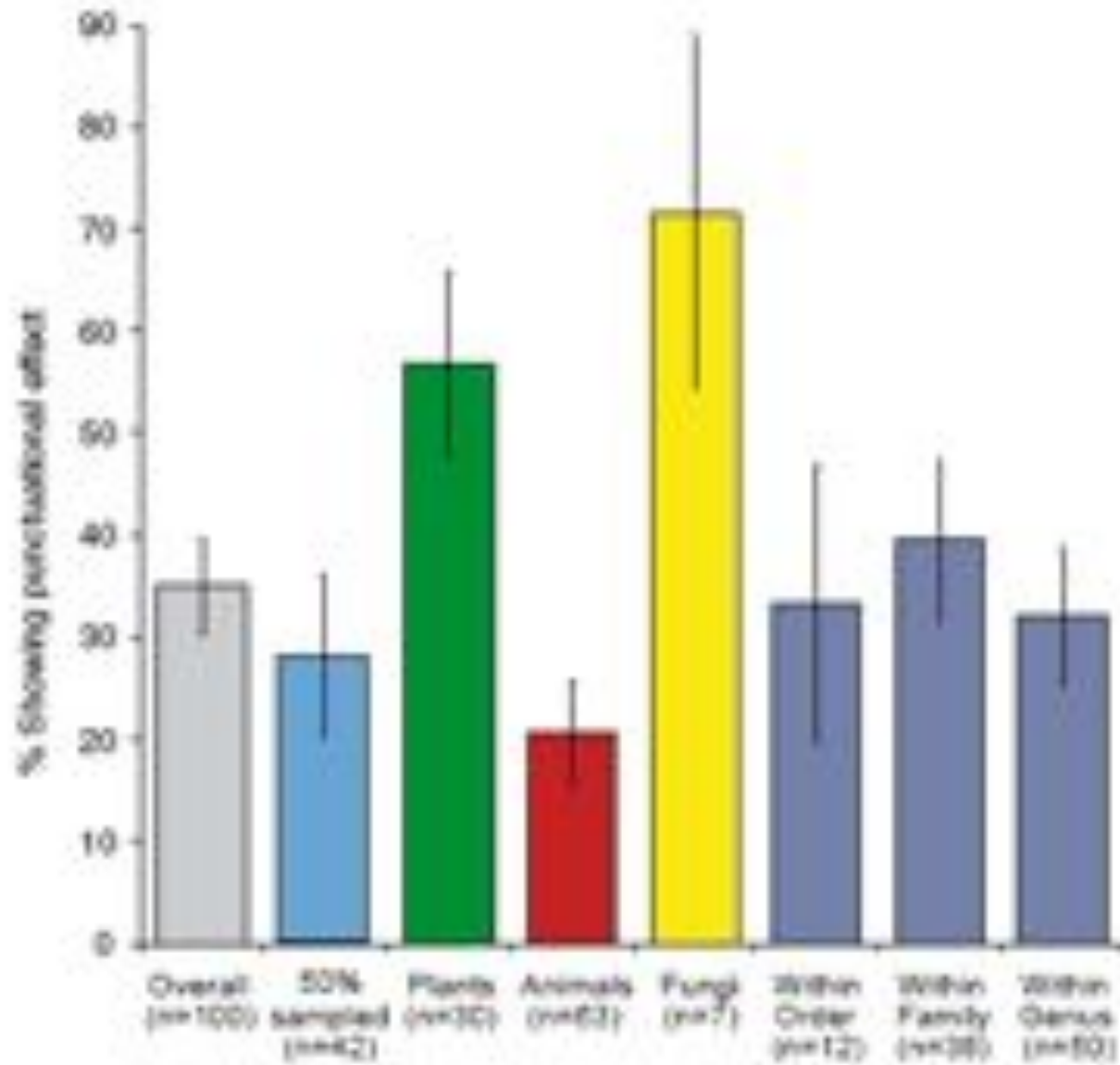
La curva ricavata da $X = n\beta + g$ cambia forma a seconda del valore di β



abbiamo trovato una relazione significativa fra numero di nodi e lunghezza del cammino (cioè, $\beta > 0$) in 57 [46.7 \pm 4.5% (\pm SE)] dei 122 alberi

- We analyzed 122 gene-sequence alignments selected for including a well-characterized and narrow taxonomic range of species.
- For each data set, we derived a Bayesian sample of the posterior distribution of phylogenetic trees
- We then estimated β from the relationship between x and n in each tree [...], using a statistical method
- we found a significant relationship between nodes and path lengths (i.e., $\beta > 0$) in 57 [46.7 \pm 4.5% (\pm SE)] of the 122 trees

Fig. 2. Percentage of data sets with evidence for punctuational evolution. The Overall data set comprises the 100 trees free of the node-density artifact. 50% sampled refers to the subset of 42 trees in which 50% or more of the known taxa have been sampled. Plants, Animals, and Fungi are the data sets representing these taxonomic groups. Within Order, Within Family, and Within Genus isolate data sets of varying taxonomic range. Apart from differences among taxonomic groups, the rate of punctuational change is relatively stable among the various subsets. Error bars indicate the standard error of the mean.



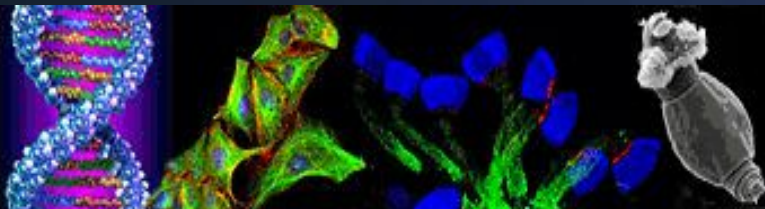
E la stasi?

Per converso, non abbiamo trovato alcuna controparte della stasi, conosciuta per i caratteri morfologici [...] Queste due osservazioni non sono in conflitto perché il cambiamento molecolare può avvenire indipendentemente da quello morfologico.

Gli equilibri punteggiati messi alla prova

Marco.Ferraguti@unimi.it

Dipartimento di
BIOSCIENZE



UNIVERSITÀ
DEGLI STUDI
DI MILANO

If these results are valid, than in the taxa in which punctuational effects are important (35% of our set) molecular clocks are badly working!!

Across the 35 data sets showing a punctuational effect, the average correlation between path lengths and nodes ranges from 0.22 to 0.69 [...]; punctuational effects contributed between 4.8 and 48% [...] of the deviation from molecular clock-like behavior in these trees

space structure of populations



Enallagma vesperum



© - josef hlasek
www.hlasek.com
Enallagma cyathigerum 2496

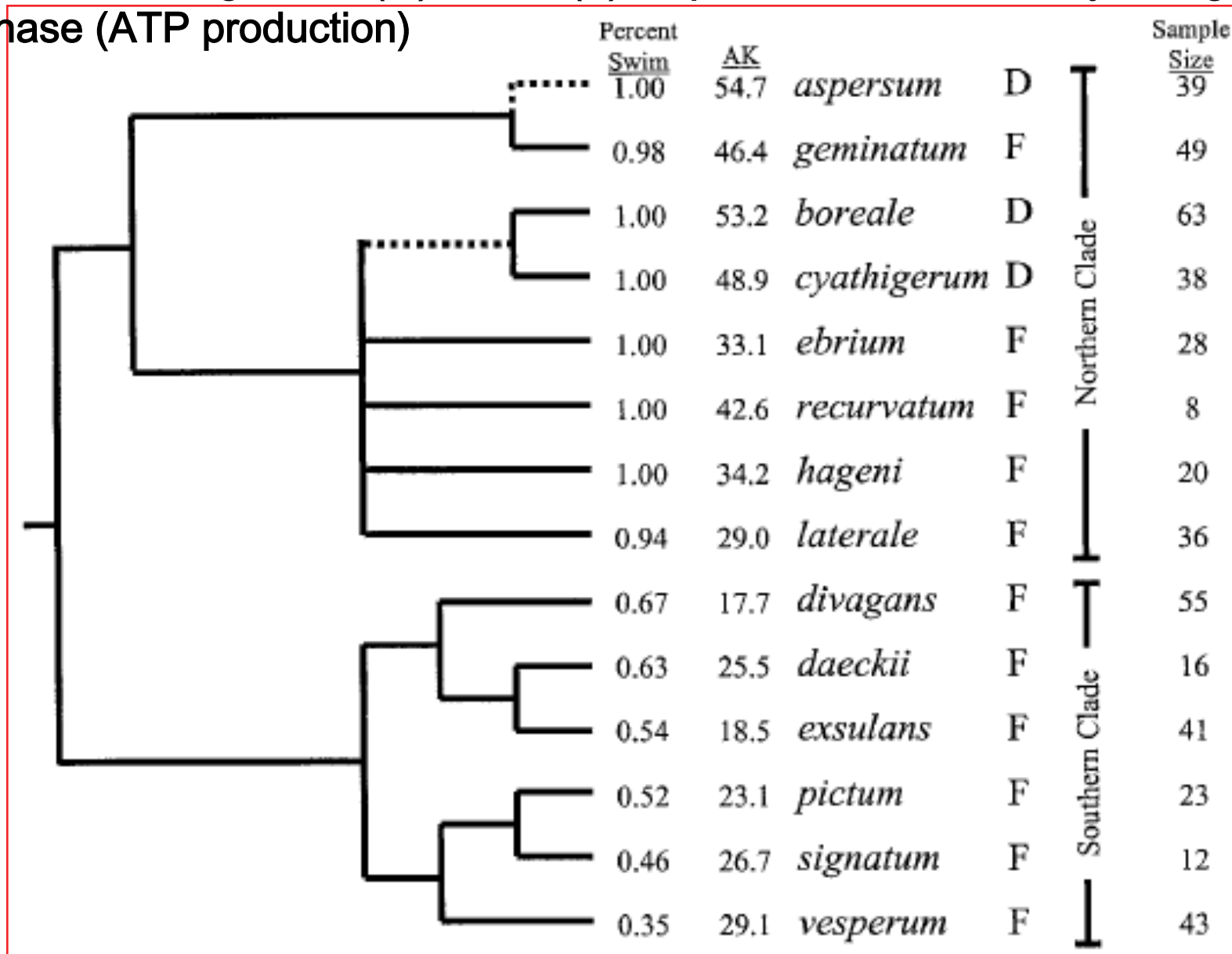
Enallagma is a dragonfly genus living originally in lakes where the predators are fishes. And their defense is mimics.

“Recently” 4 species (of a single clade) over 38 have invaded lakes where the predators are other dragonflies, and the larvae have evolved the ability to escape by swimming.

This ability is already present to a certain extent in the species from which they derived!

McPeck, *Evolution*, 54, 2072, 2000

Phylogenetic tree (mitochondrial DNA) of some *Enallagma* spp. living in lakes with dragonflies (D) or fish (F) as predators; AK= activity of arginin kinase (ATP production)



These habitat shifts have been accompanied by rapid evolution in a number of morphological, behavioral, and biochemical characters that enhance burst swimming speed because of selection imposed by dragonfly predators in the new environment.

It may have taken the invading lineages only a few hundred years to gain a high degree of local adaptation to their new environment.

Such rapid evolutionary change would appear saltatory in the fossil record. In contrast, rates of evolution in these characters within the fish lake environment are very slow.

Importantly, shifts to dragonfly lakes and accompanying rapid evolution have been rare events, occurring in only one of the two primary clades of *Enallagma*. That clade has a number of phenotypic characters that are already similar to phenotypes favored by selection in dragonfly lakes.

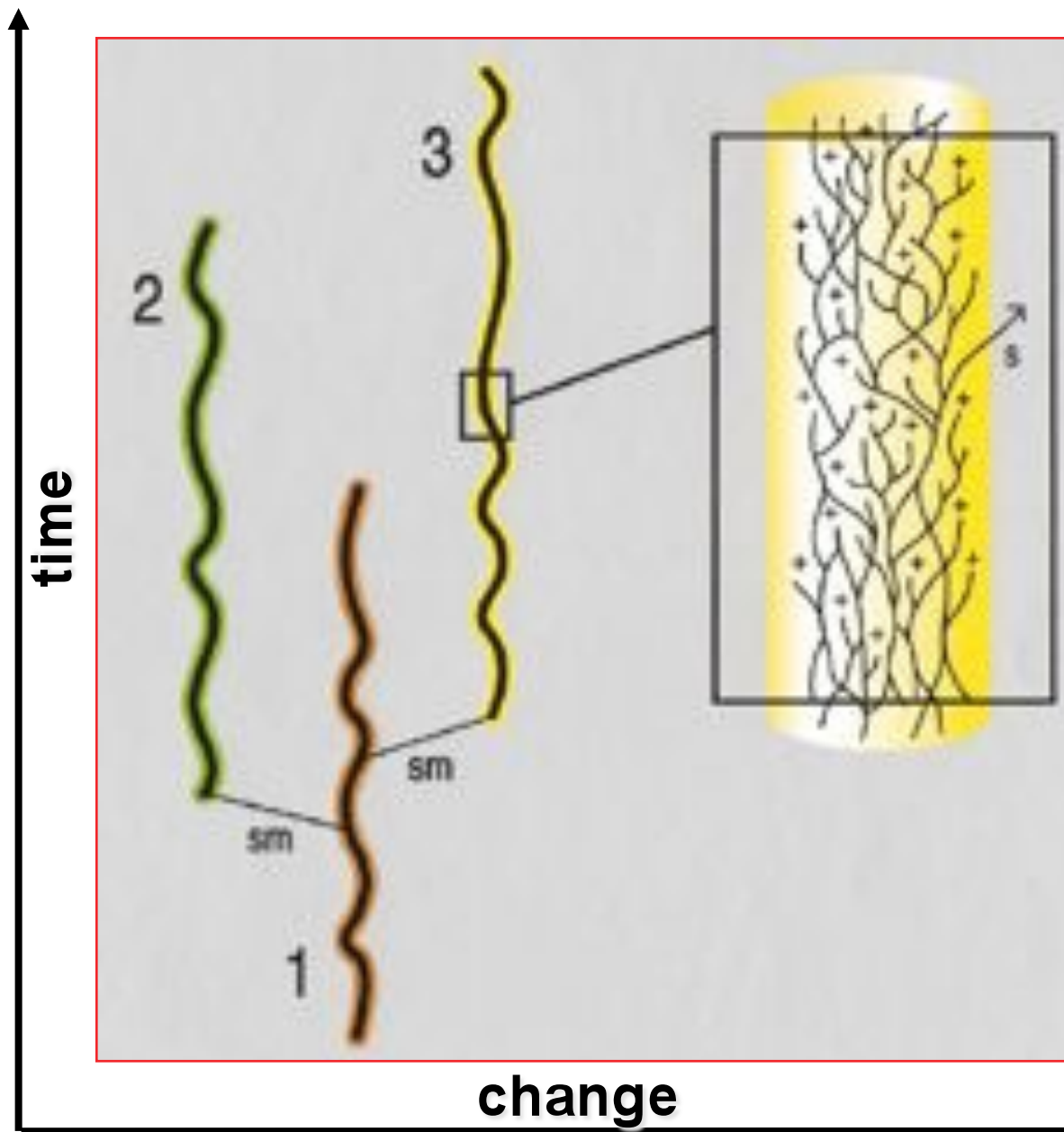


FIGURE 1. Species (lineages 1, 2, and 3 on the left) exhibit negligible net phenotypic changes, while their component population systems (on the right) continually differentiate, fuse, or go extinct. Stasis is occasionally broken by establishment and spread of novel phenotypes (s); when this is matched with ecological opportunity, highly differentiated new lineages (sm) may be formed that eventually develop internal (population) dynamics and geographic structure resulting, again, in stasis. (In this view, species-lineages consist of anastomosing population systems and, at the same time, belong to clades composed of similar lineages)

Do species populations really start small? New perspectives from the Late Neogene fossil record of African mammals

E. S. Vrba^{1*} and D. DeGusta²

¹*Department of Geology and Geophysics, Yale University, PO Box 208109, New Haven, CT 06520-8109, USA*

²*Department of Anthropological Sciences, Stanford University, Stanford, CA 94305-2117, USA (degusta@stanford.edu)*

This analysis of all known African larger mammals of the past 10 Myr offers new perspectives on the geographical circumstances of speciation. Our central question is: does the fossil evidence support the idea that most new species start as small populations and, if true, how long is the average growth interval until species are established at their mean later size? This simple question is important to unravelling the competing claims of rival models of speciation. We approached it by direct use of fossil data, which, to our knowledge, has not been done previously. We compared the numbers of fossil site records, as a proxy for magnitude of geographical spread, between survivorship intervals across all species. The results show that the average mammal species has indeed started its life in a relatively small population, and thereafter increased rapidly in geographical spread to reach its long-term equilibrium abundance by about 1 million years after origin. Some theoretical implications of these results are discussed.

survivorship category	average <i>sr</i>
<i>f</i>	1.91
<i>s</i> 1	3.18
<i>s</i> 2	3.96
<i>s</i> 3	3.60
<i>s</i> 4	3.25
<i>s</i> 5	3.48
<i>s</i> 6	3.67
<i>s</i> 7	3.73
<i>s</i> ≥ 8	2.50
Σ	

Representation in the African fossil record, 10 Ma to Recent, of larger mammal species in survivorship categories. (The columns represent numbers of site records ($sr = x$) per species per 0.5 Myr-long intervals (10 t 9.5 Myr, ...0.5 t 0 Myr). The entries in the *sr* table are total numbers of instances of species with $sr = x$, across all species recorded in each survivorship category: *f*, first appearance in a 0.5 Myr-long interval; *s*1, survivor recorded in the interval immediately succeeding the *f*-interval, and so on; average *sr*, average site record number;

2058 site records for 259 species

By introducing a correction factor transforming the data on fossil record in data on the “real world”, the analysis gives results closed to 1

Gli evoluzionisti misurano l'evoluzione (ad esempio) con un'unità di misura chiamata darwin

Misura del carattere X
al tempo T2

Misura de carattere X
al tempo T1

$$\ln X_{t2} - \ln X_{t1}$$

$$d = \frac{\quad}{\Delta t}$$

Tempo intercorso fra T1 e T2
(in milioni di anni)

(T1 = tempo più antico; T2 = tempo più recente)

Morphological evolution is accelerated among island mammals

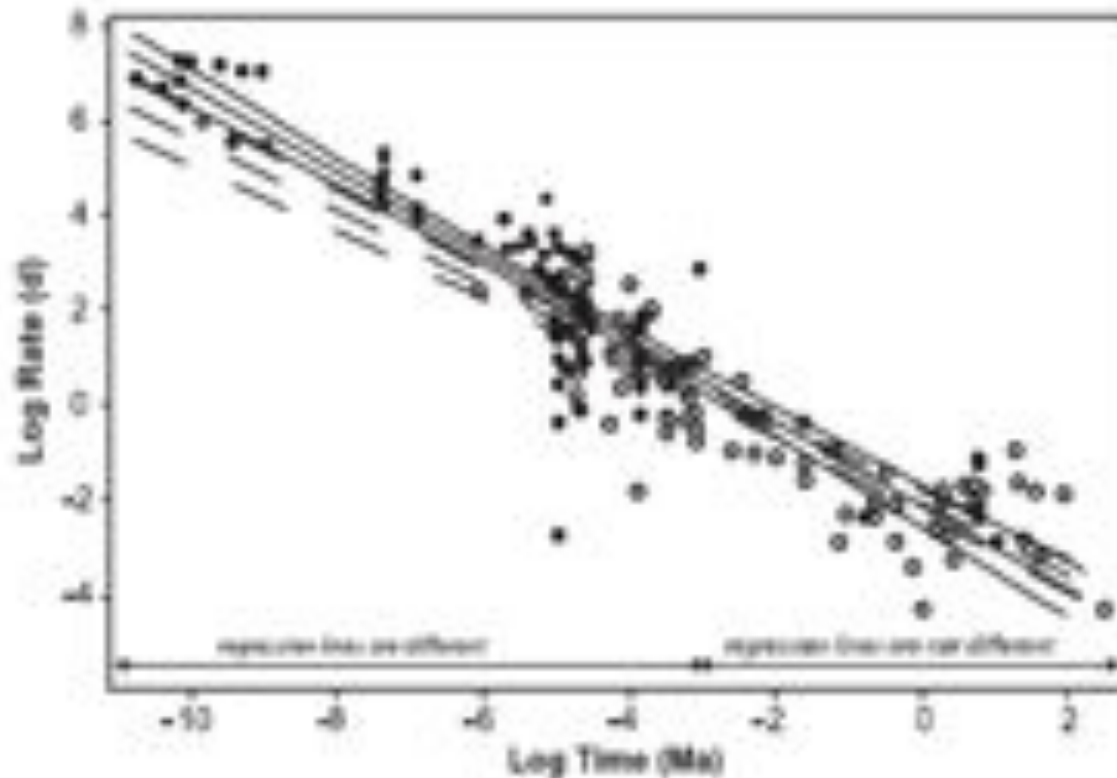


Figure 2. Relation between Evolutionary Rates (Mean Values, darwins) and the Time Interval (Million Years) over which They Were Calculated. Filled circles: islands, open circles: mainland; the regression line for islands (solid line) is above the line for the mainland (dotted line). The 95% confidence intervals of the two regression lines do not overlap between the two groups at the smallest time intervals. The difference in elevation (i.e., the rate difference) between the two lines is statistically significant below 0.25 million years.
DOI: 10.1371/journal.pbio.0040321.g002

the regression line connecting the data form islands (solid) is higher than that of mainland (dotted) when time intervals are shorter

... in 60 original publications. The dataset comprised 170 populations of 88 species or evolutionary lineages, belonging to 14 orders of mammals, and a total of 826 evolutionary rates were calculated

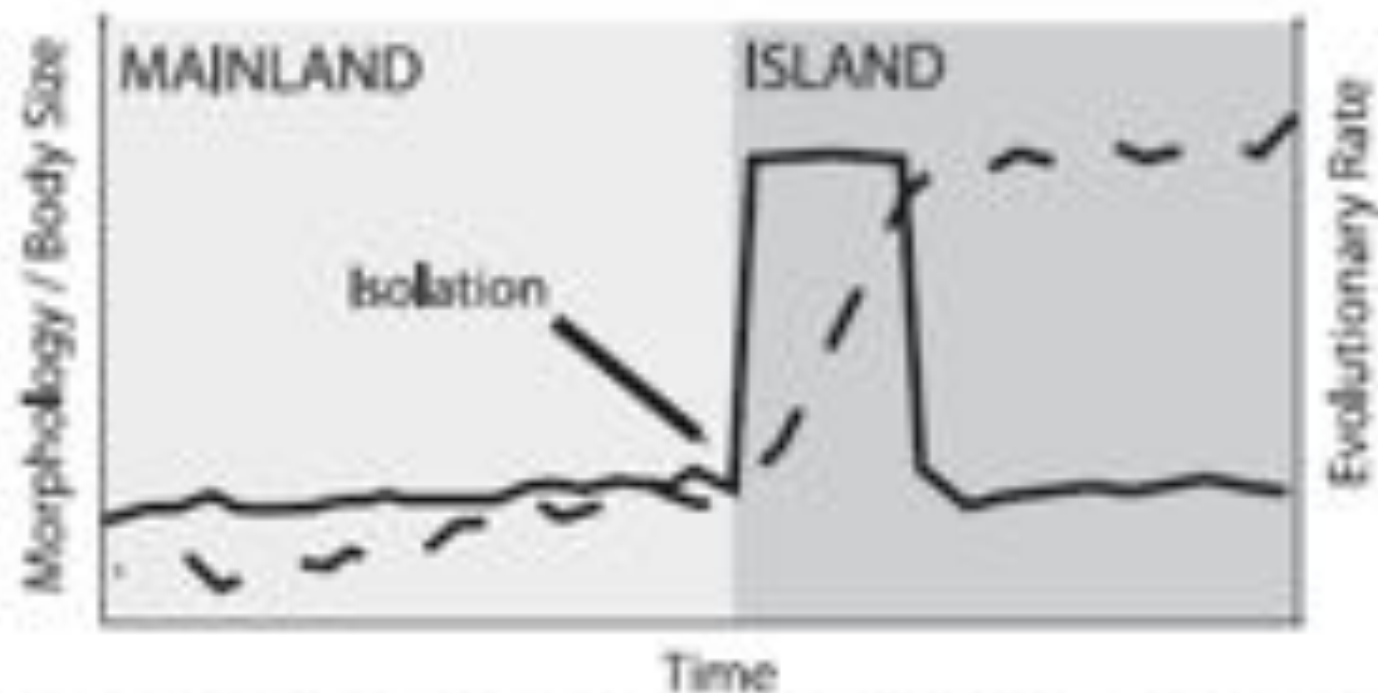


Figure 4. Evolution of the Size of a Morphological Character (Solid Line) in a Hypothetical Population

The character size of the ancestor population from the mainland increases by a small amount on the mainland. After the isolation of the population, there is a large and rapid increase of the size of this character, and the evolutionary rate (solid line) for this character also increases. The rate of evolution on the island then decreases to values comparable to the rate values for the mainland population.

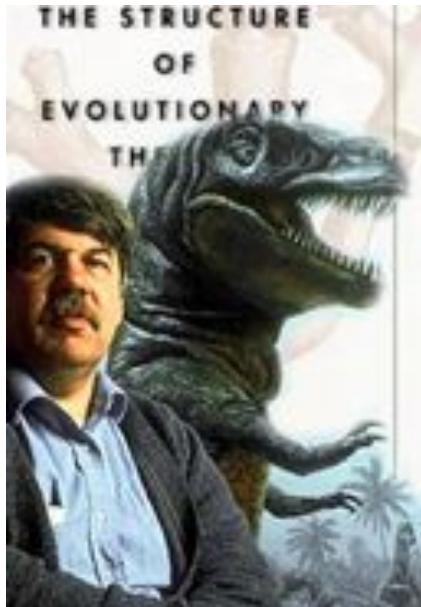
DOI: 10.1371/journal.pbio.0040321.g004

Punctuated Equilibria—Where is the Evidence?

PHILIP D. GINGERICH

Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109

to gradualism. Perhaps the time has come to end this false debate and concentrate instead on study of the rates and patterns we can observe.



The empirics of punctuated equilibrium

Punctuated equilibrium surely exists in abundance, but validation of the general hypothesis requires a relative frequency sufficiently high

**S.J.Gould & N. Eldredge Punctuated equilibrium comes of age.
Nature, 366, 223, 1993**

*"It was twenty years ago today
Sgt. Pepper taught the band to play. . ."*



*Here is a hero who did nothing
but shake the tree when the fruit
was ripe. Do you think that was a
small thing to do? Well, just look
at the tree he shook. (Skeptic, 1, 1992)*