

The origins of modern biodiversity

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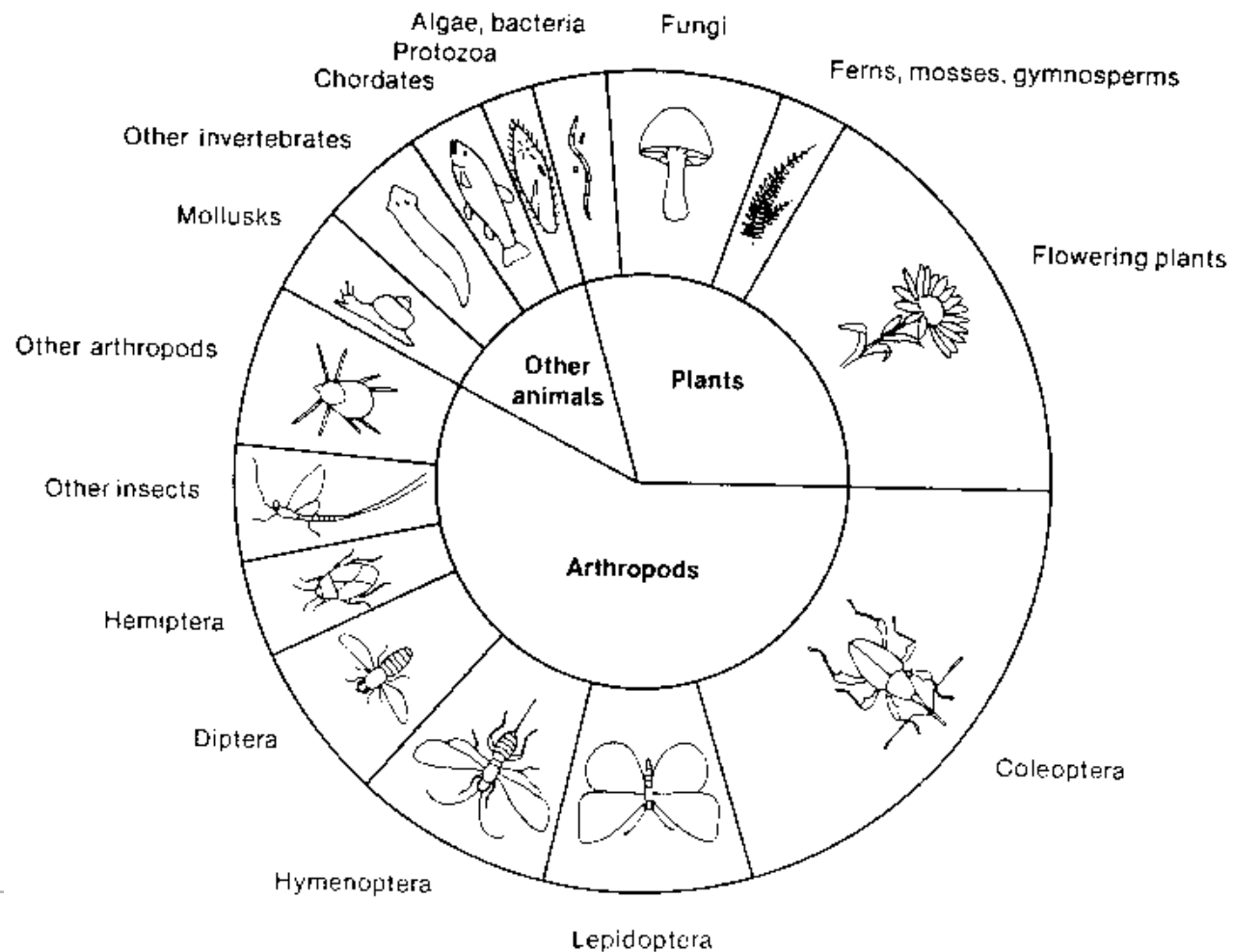
Bright Horizons 10

Friday, October 7th, 2011

Origins of biodiversity

1. What is current biodiversity and extinction loss?
2. Patterns: how did life diversify to its current level of 10M+ species? Slowly and steadily, or relatively rapidly in the last 100 Myr?
3. Processes: is diversification driven by **extrinsic** (abiotic/ physical) changes in the environment, climate, or land surface, or are **biotic interactions** more significant? Balance of climate and other external forcing factors and innate biological drivers.
4. Does biodiversity expand by specialization or co-option of new ecospace, or is the rise promoted by external environmental drivers (or a little of all three)?

Modern biodiversity

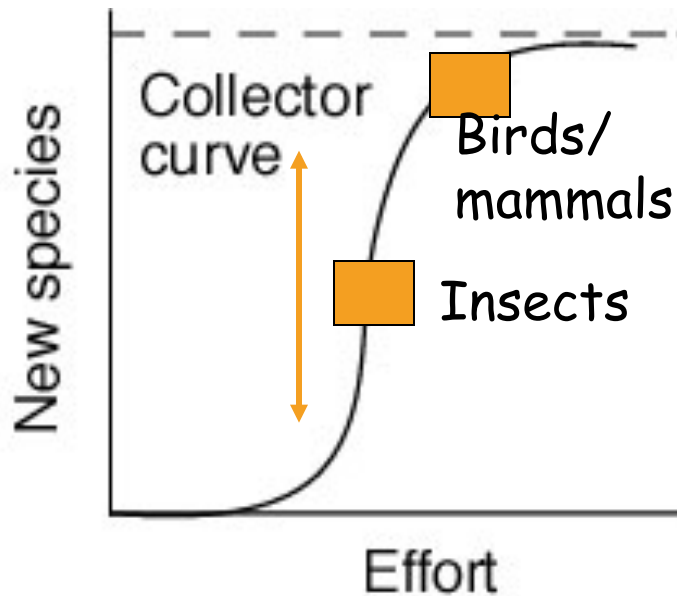


How many species? 1

- Some 1.8M species have been named
- But at least 0.4M of these are synonyms...
- leaving 1.4M valid named species
- So how many are out there waiting to be named? 5M?



How many species? 2



- Two or three new species of birds and mammals are named each year
- But some 7500 new species of insects are named each year
- So maybe we know pretty well all the species of birds (10,000) and mammals (5000)
- But, at this rate, there are probably many more than the 750,000 named species of insects

How many species? 3



- Terry Erwin (1980) adopted a sampling approach
- He blasted one species of tropical tree and collected all the beetles
- He picked up 1100 species of beetles from the tree, of which 160 were unique to the tree species
- He estimated 160 unique beetles = 600 unique arthropods
- There are some 50,000 species of tropical trees
- So, $50,000 \times 600 = 30\text{M}$ species of tropical terrestrial arthropods

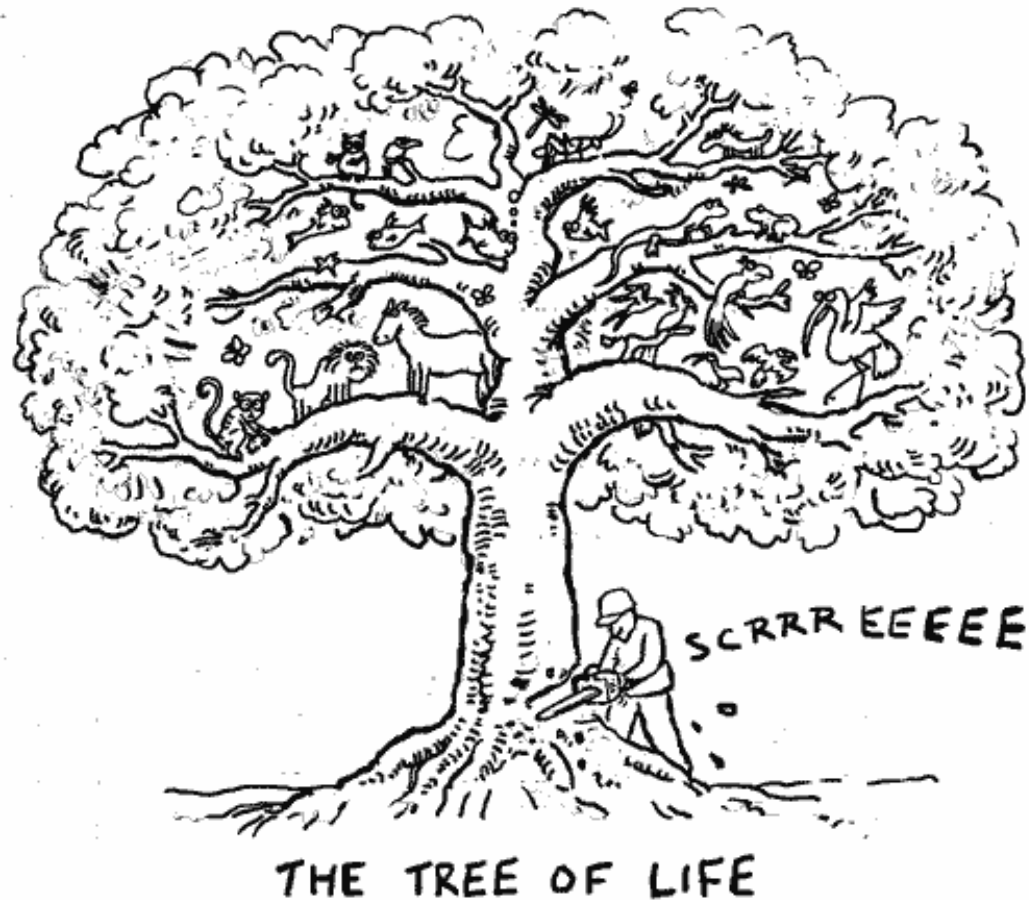
How many species? 4



- 30M species of terrestrial tropical arthropods = 50/100M species of organisms altogether
- So are there 5M species (conservative/ taxonomic estimate) or 100M?
- Recent work (Novotny *et al.*, 2002) shows much lower host specificity
- The 30M reduces to 4-6M
- So total global diversity then scales down from 50-100M to 6-20M
- So maybe 10-15M altogether

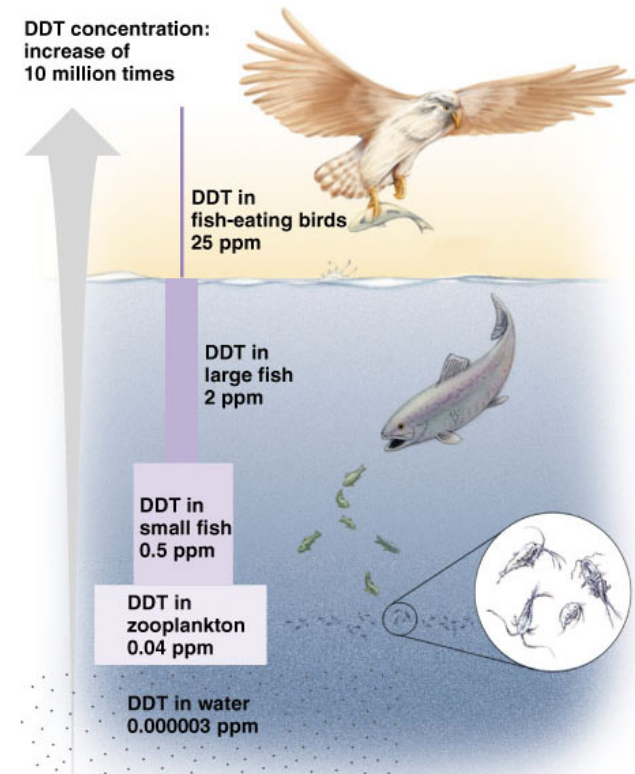
Why is biodiversity important?

- Aesthetic
- Ethical
- Crops, fibres and medicines
- Ecosystem services (\$33 trillion/year)
 - Purification of air and water
 - Nutrient cycling
 - Protection from ultraviolet rays



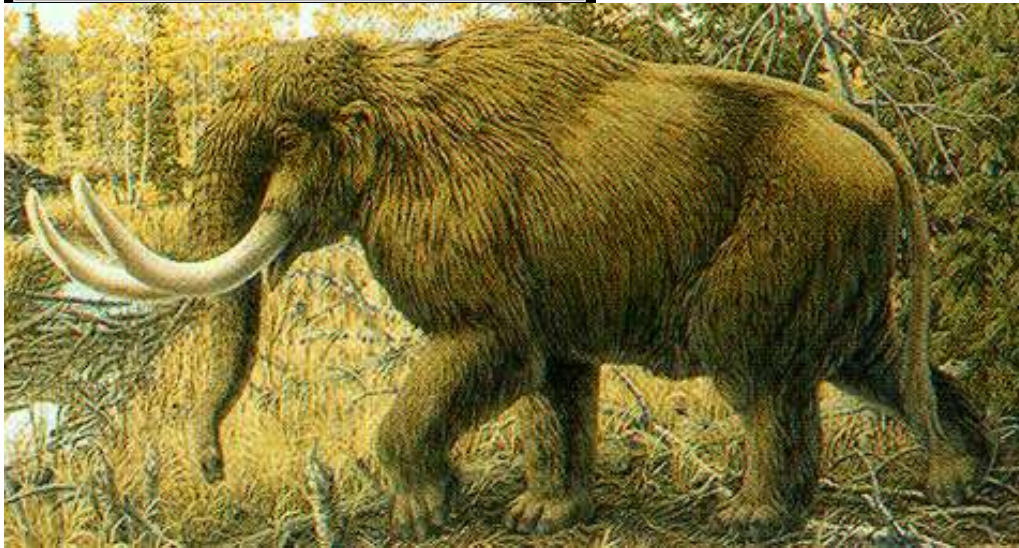
The human impact on biodiversity

- Habitat destruction
- Habitat fragmentation
- Introduced species
- Overexploitation
- Disruption of food chains



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The most recent extinction event



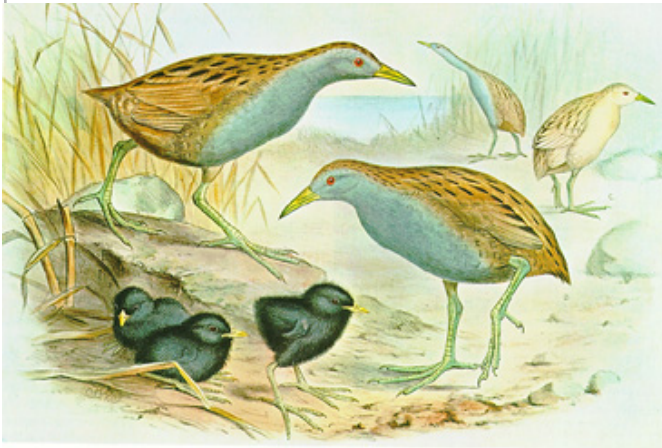
- Extinction at end of the Pleistocene (11,000 years ago)
- Extinctions of large mammals on most continents
- Mammoths, mastodons, woolly rhinos, giant marsupials, giant ground sloths, sabre toothed cats... died out
- But little effect on other animals and plants



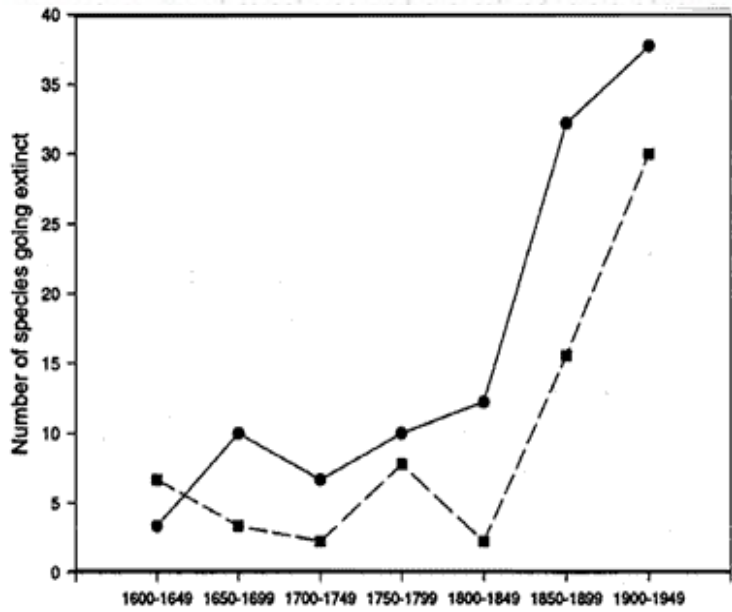
Hawaiian rail



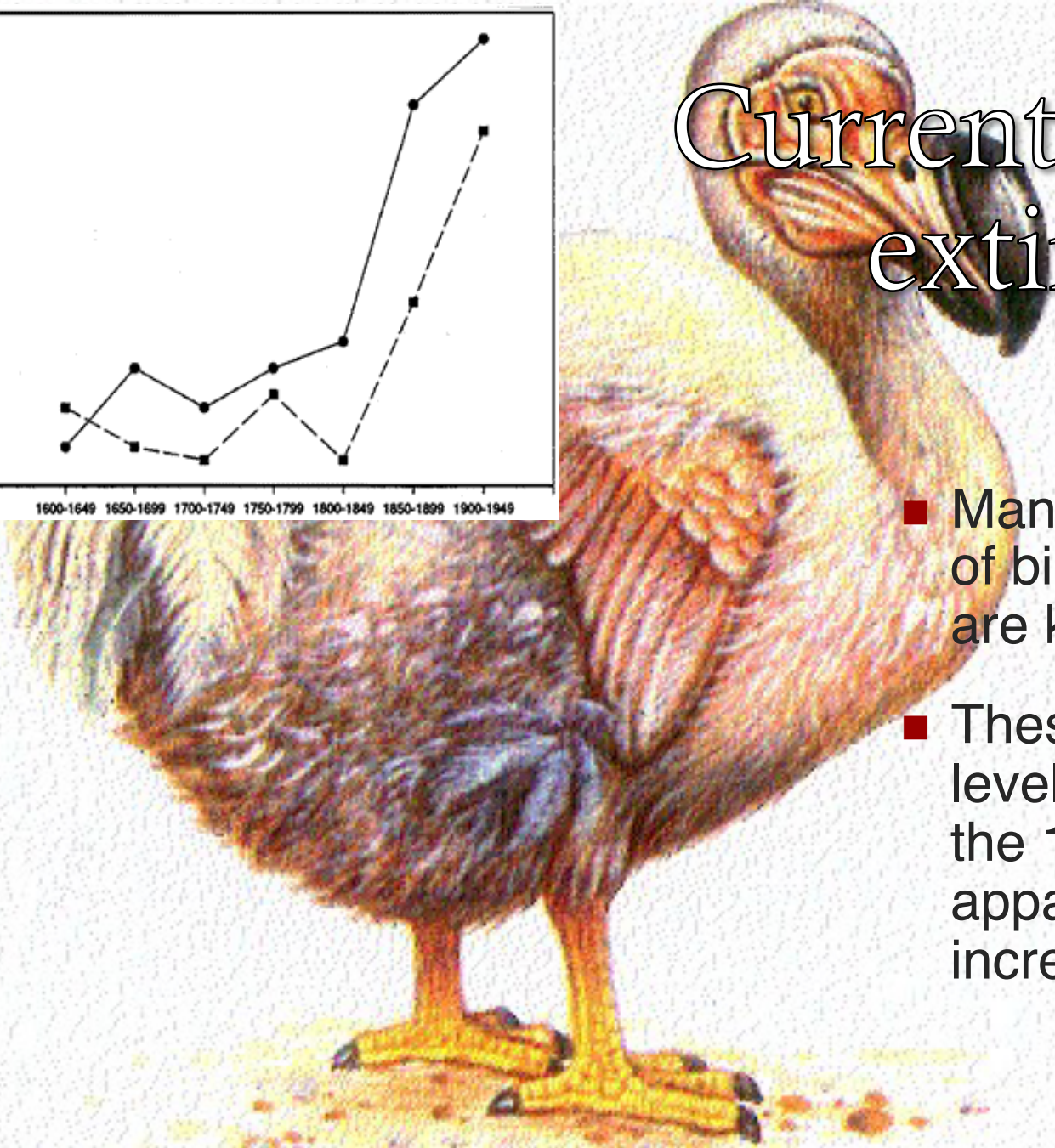
Lanai
hookbill



Current rates of extinction 1



- Many dated extinctions of birds and mammals are known
- These indicate low levels of species loss in the 17th century, but an apparently exponential increase since then



Current rates of extinction 2



- Current risks of extinction are 5-10 times greater on islands than on continents
- Current rates of extinction are proportional to human population size in an area and to degree of industrial development

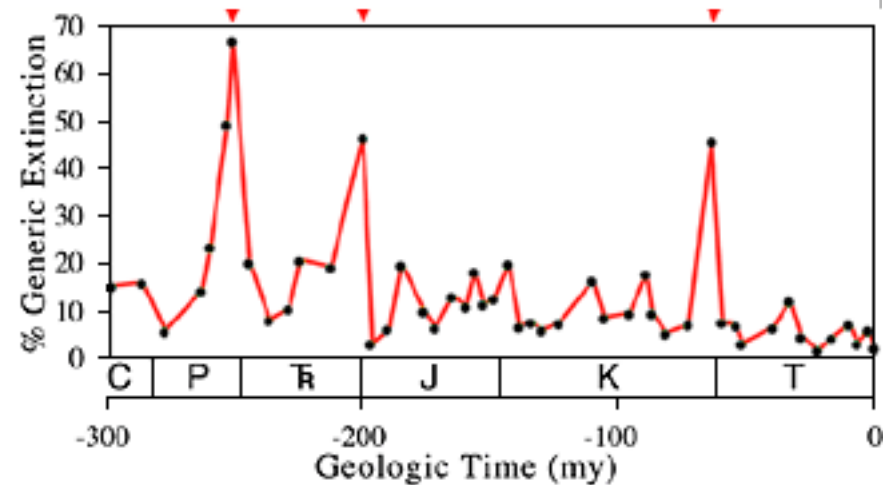
Current rates of extinction 3

- So what is the current rate of species loss?
- Rates for birds and mammals are 0.1-0.3% per annum...
- 0.3% of 10M is 30,000 species lost per annum ... which is 80 species per day
- 0.3% per annum means the extinction of all life in 300 years



Current rates of extinction 4

- 0.3% per annum also scales to **3000% per million years** - the biggest mass extinction of all time!
- But is the 0.3% rate an overestimate applicable only to marginal species of birds and mammals?

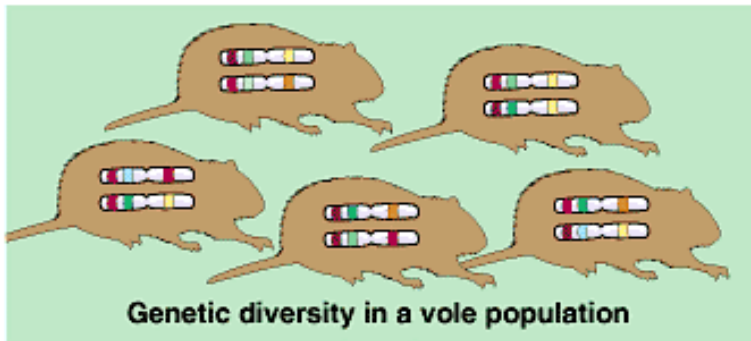


What about cockroaches...
and humans?

The future



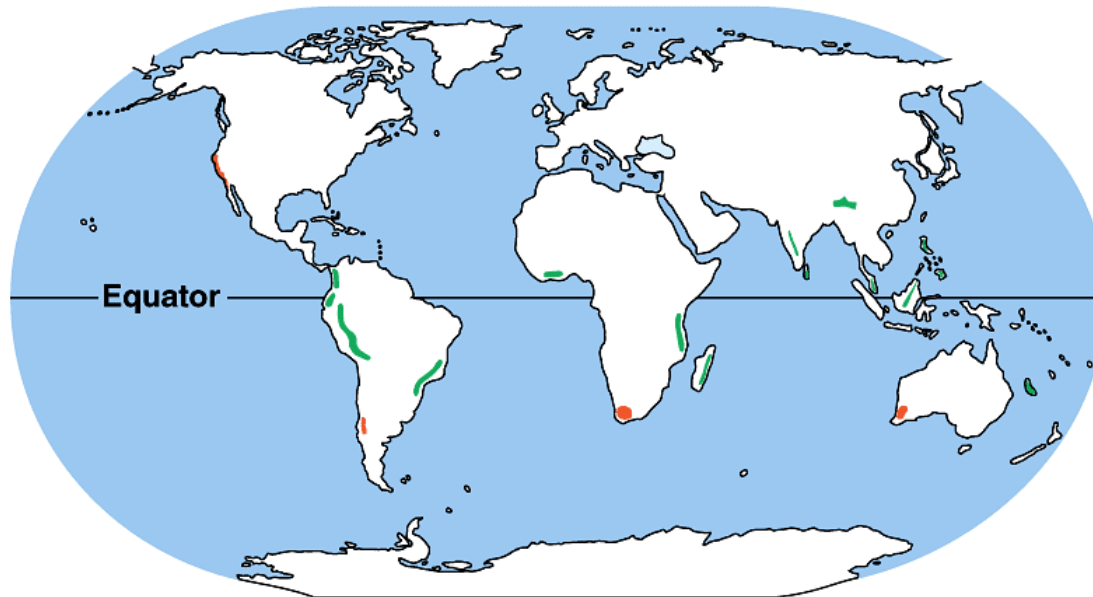
- Past mass extinctions prove that life can recover
- After mass extinctions, life passed through a **bottleneck** where only 10-50% of species survived
- These founders were a random group - no selectivity
- Recovery: **disaster species**, cosmopolitan, may take 10-50 My to recover full ecosystem complexity



Conserving biodiversity

- **Extinct** species: those that are gone from the planet
- **Threatened** species: those likely to become endangered in the foreseeable future
- **Endangered** species: those in danger of extinction throughout most of its range

Biodiversity hotspots



 Tropical forest hot spots

 Chaparral hot spots

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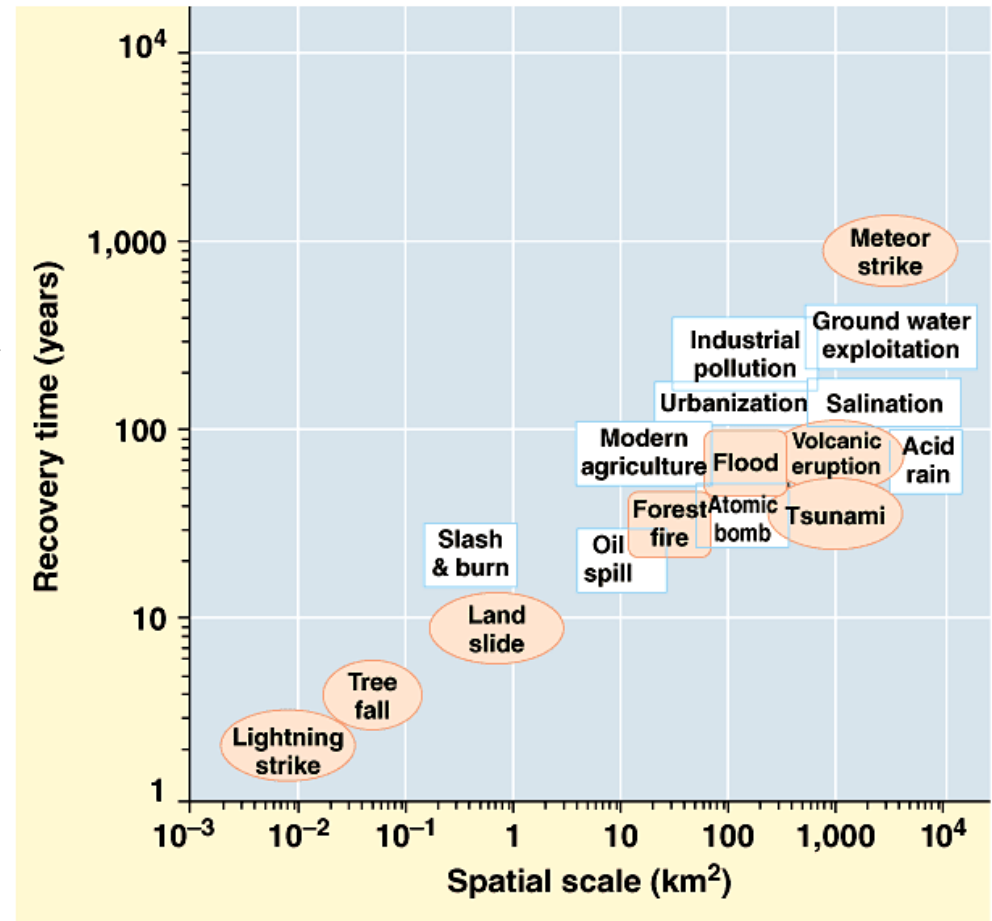
A **biodiversity hotspot** is a region with unusually high diversity of endangered species - mainly tropical.

Levels of conservation

- Small population: of conservation concern because of the small population size in itself can drive extinction
- Declining population: of conservation concern because of the loss of individuals → potential extinction
- Biologists work out the Minimum Viable Population (MVP; c. 1000 for a bird or mammal species): two Californian condors is enough to make a baby, but not enough to preserve the richness of the **gene pool**
- Knowing the MVP then identifies the minimum range/ reserve size for that species

Recovery and restoration

- Disasters may be natural (pink) or human-induced (white)
- Time to recovery is proportional to magnitude of disaster
- Frequency of occurrence of natural disasters usually inversely proportional to magnitude...
- But, as for human-induced disasters?



“Right now, we’re pushing the species of the world through a bottleneck. We’ve got to make it a major moral principle to get as many of them through this as possible. It’s the challenge for now and for the next century. And there’s one good thing about our species: We like a challenge!”

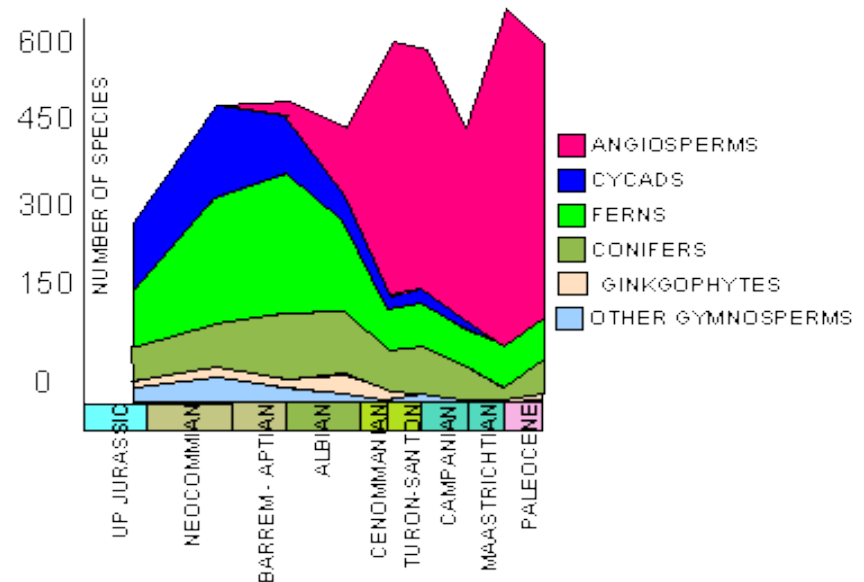
– E.O. Wilson

Life on land

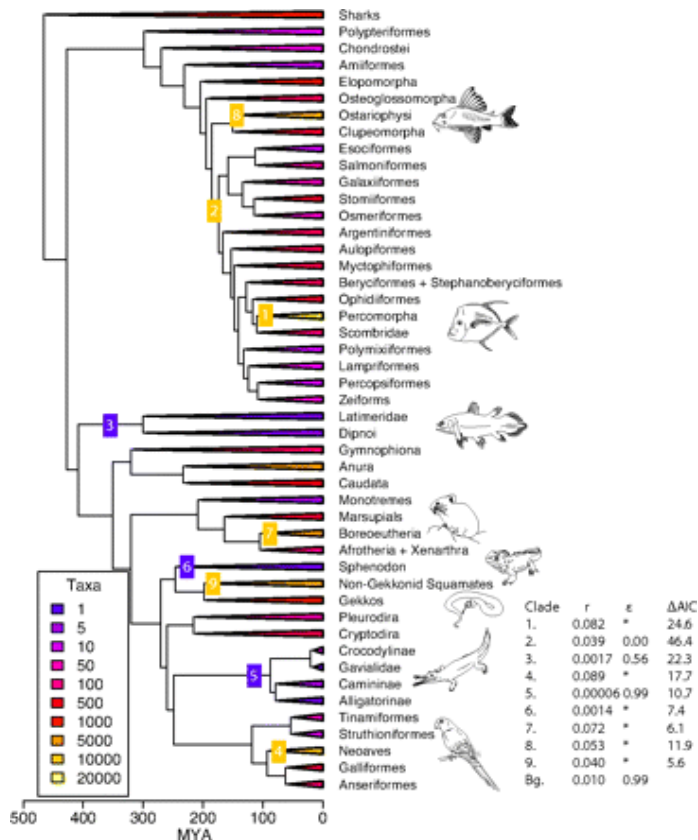
- Life on land today accounts for 85% of living species (c. 10 million species; largely insects, flowering plants, spiders, and vertebrates; May 1990; *Phil. Trans. B*)
- Life in the sea, many millions of years ago, comprised a higher proportion than now, and the changeover seems to have happened 100-125 Mya, during the Early Cretaceous (Vermeij & Grosberg 2010; *Integr. Biol.*)
- This time of massive expansion was the Cretaceous Terrestrial Revolution (KTR; Lloyd *et al.* 2008, *PRSB*)

The Cretaceous Terrestrial Revolution

- Angiosperms (flowering plants) appeared in the Early Cretaceous and diversified rapidly
- We name the KTR as an analogue of the Mesozoic Marine Revolution (MMR), a term devised by Vermeij (1987)
- The KTR was the explosive diversification of angiosperms, herbivorous and social insects, squamates, birds and mammals... dinosaurs were not a part of the KTR(?)

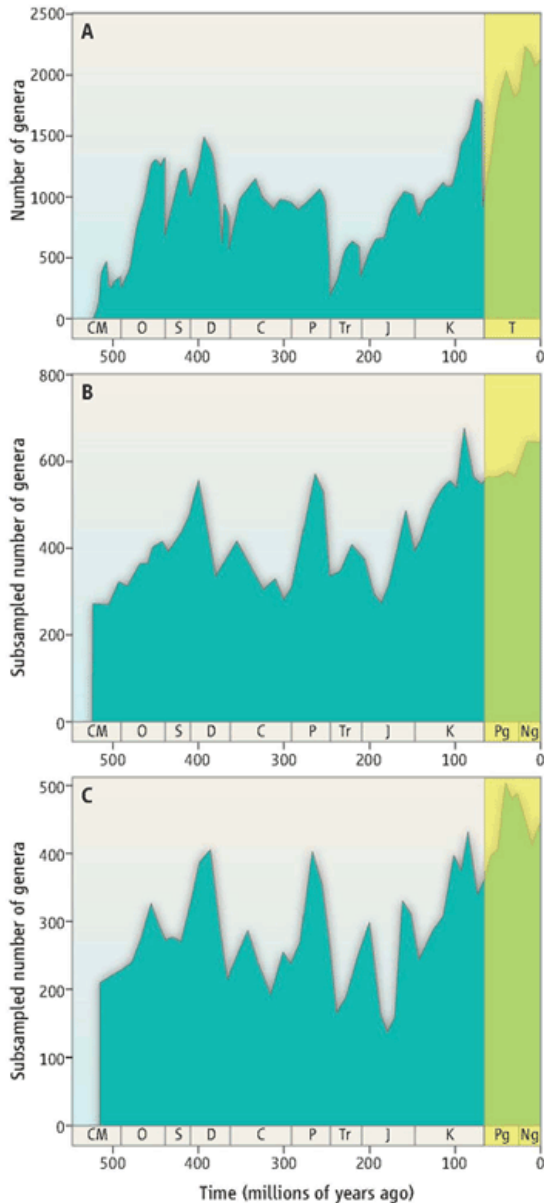


Expansion 1



- Perhaps there was a real and massive expansion of life in the sea following the MMR, and on land following the KTR
- Evidence from phylogenetic studies (both morphological and molecular) that show the most speciose clades of modern macro-life (e.g. angiosperms, ants, bees, teleost fishes, birds) arose 100-150 Mya (e.g. Alfaro *et al.* 2009, *PNAS*)
- This matches timings from the fossil record

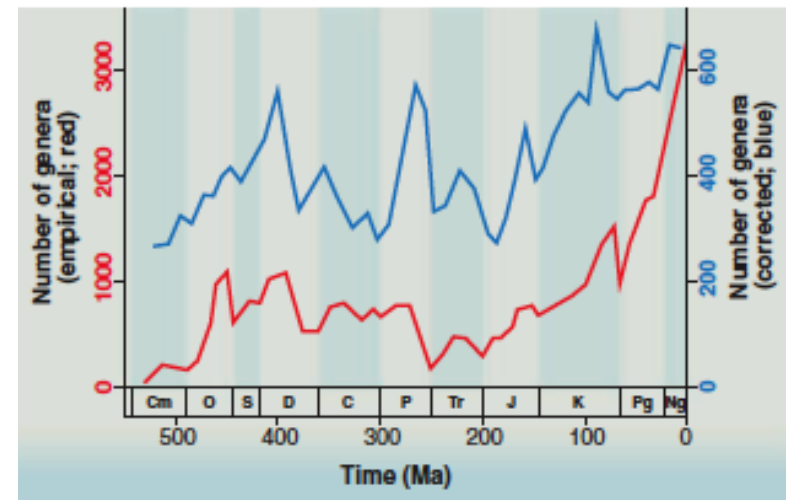
Expansion 2



- This model of massive biodiversity expansion in the past 100 Myr has been strongly disputed
- Sepkoski (1984) found the rise in his famous plot of marine diversity through time (top)
- However, Alroy *et al.* (2001, 2008) found no such rise (middle), although the rise returns modestly in Alroy (2010) (bottom)
- The Alroy studies depend on different methods of sampling standardisation (a reasonable thing to do), but perhaps the better-quality fossil records of the past 100 Myr are ‘punished’ too much

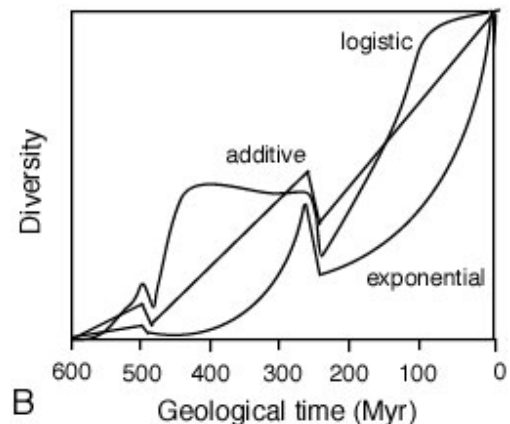
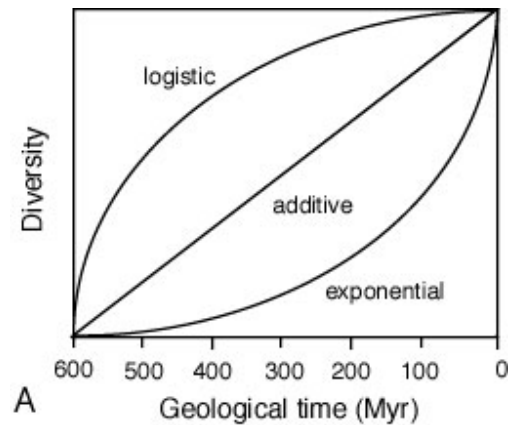
Diversity and the fossil record

- Can we read the fossil record literally, or is it biased? The two current views (right) reflect a long-running debate
- The blue curve (Alroy *et al.* 2001, 2008, *Science*) has been corrected by **sampling standardisation**, methods that modify species counts in collections to account for different intensities of sampling
- The red curve (Benton 1995, *Science*) shows the uncorrected (empirical) pattern
- Probably the truth lies somewhere between these two



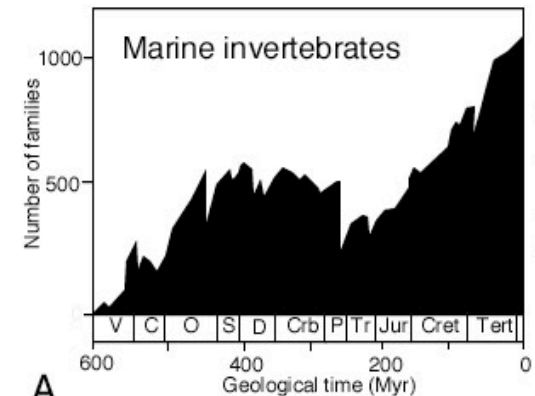
Models 1

- There are many possible models of global diversification:
 - Additive (regular stepwise addition)
 - Exponential (regular doubling)
 - Logistic (rapid rise, then asymptote)
- In reality, any of these easily distinguishable curves will be affected by vicissitudes of history, such as mass extinctions
- They also very much depend on the taxic scale (i.e. species/ genera/ families)

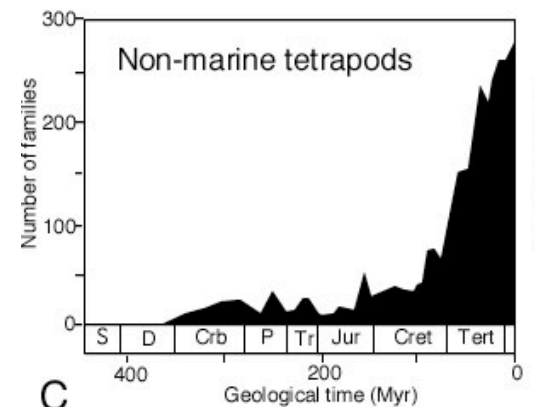


Models 2

- The debate continues...
- Certain parts of the fossil record (e.g. marine animals) follow somewhat logistic curves; others (e.g. life on land) follows a decidedly exponential pattern
- The difference may be real, or it may hinge on the degree to which error is assumed and corrected for
- Note further that these plots are at family level, not species level – if the species : family ratio changes through time, then the ‘real’ diversification curves might be very different (e.g. logistic --> exponential)



A



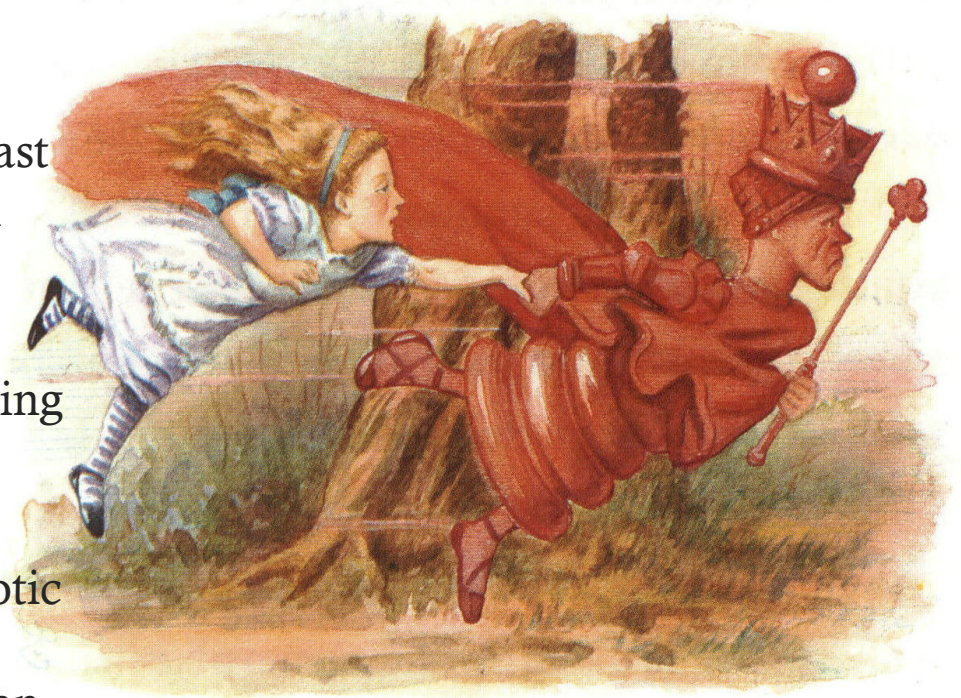
C

Recap: massive expansion of biodiversity...

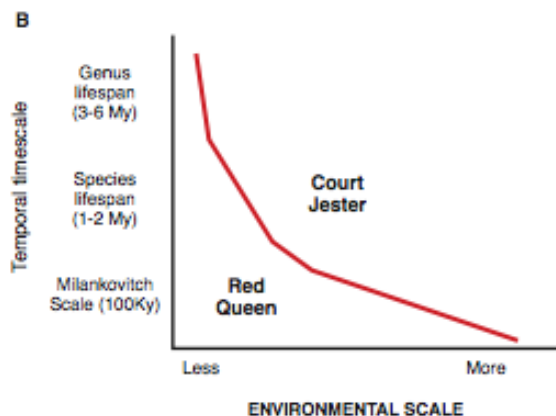
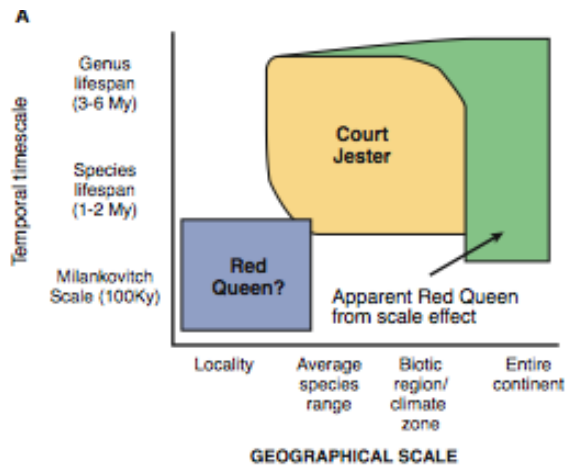
- Palaeontologists strongly debate whether life expanded to near-modern levels 500 Myr ago or 100 Myr ago
- Perspective from life on land strong suggests massive expansion linked to the rise of angiosperms 100 Myr ago
- Molecular phylogenetic data also strongly supports this explosive rise in global biodiversity on land 100 Myr ago – only negated if we argue there were 30,000 species of non-teleost fishes or 1M species of non-social insects in the Jurassic...
- Hard to disprove the latter because the fossil record can always be said to be poor... but how long do we go on hunting for these illusory missing fossils?
- What drives diversification?

The Red Queen's Hypothesis

- “Now here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that.” Lewis Carroll (1865) *Through the Looking-glass*
- Van Valen's (1973) famous RQH: organisms must be constantly evolving to remain adapted to a constantly changing environment
- The focus is on competition and biotic interaction as the key driver of macroevolution - a simple Darwinian model, scalable to all taxic levels



Biotic vs. abiotic factors?

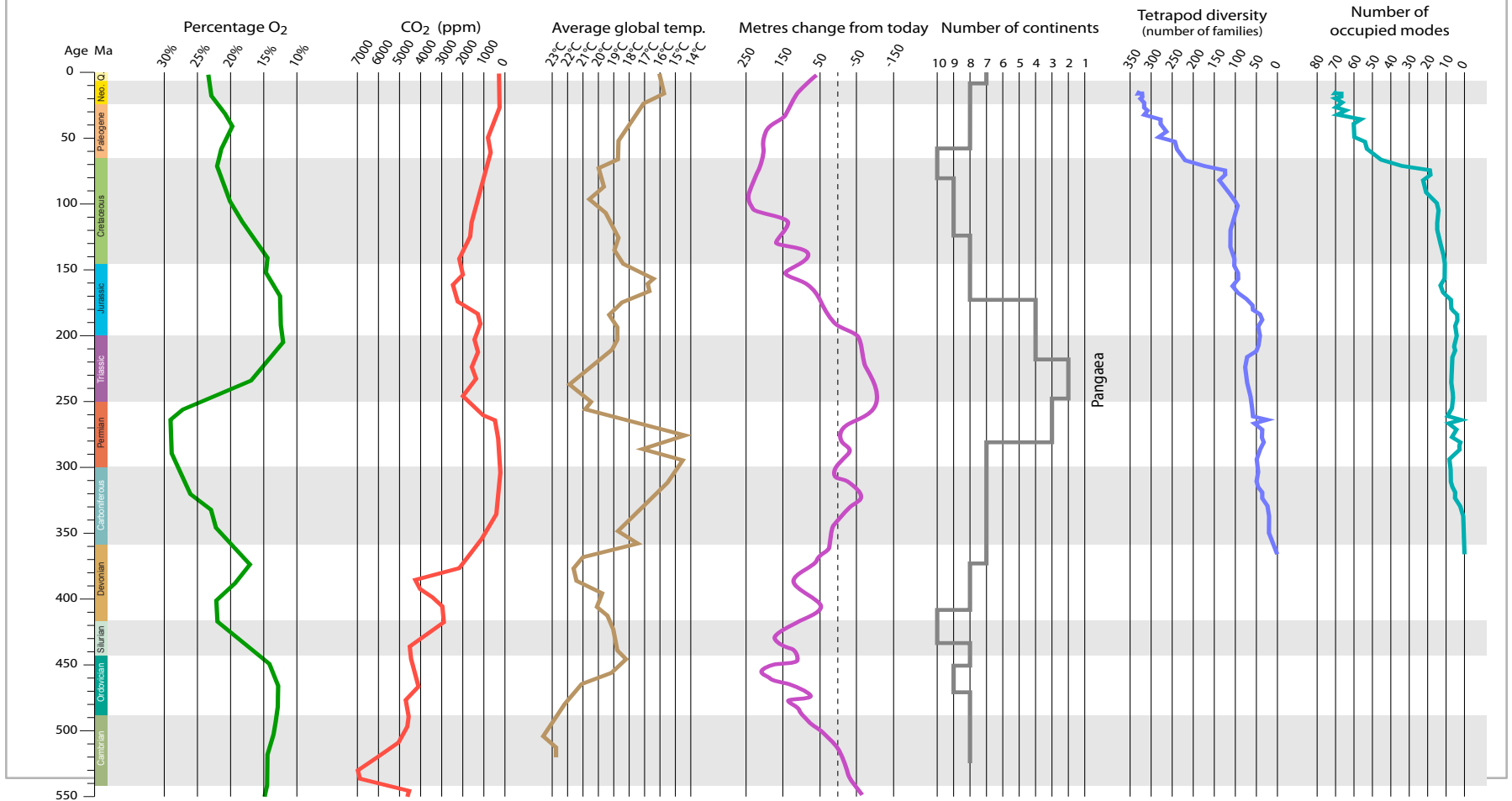


- There has been a long-running discussion about major influences on the evolution of life - biotic or abiotic
- Is this an epistemological question - biologists focus on biotic interaction, whereas palaeontologists focus on physical environmental change?
- Or is it real? Perhaps biotic interactions (competition, predation) matter at small scales, but the large features of evolution (clade expansions and contractions) are mediated by changes in climate, topography, continental position...
- The 'Red Queen vs. the Court Jester' (Barnosky 2000 *JVP*; Benton 2009 *Science*)

Major patterns through time 1

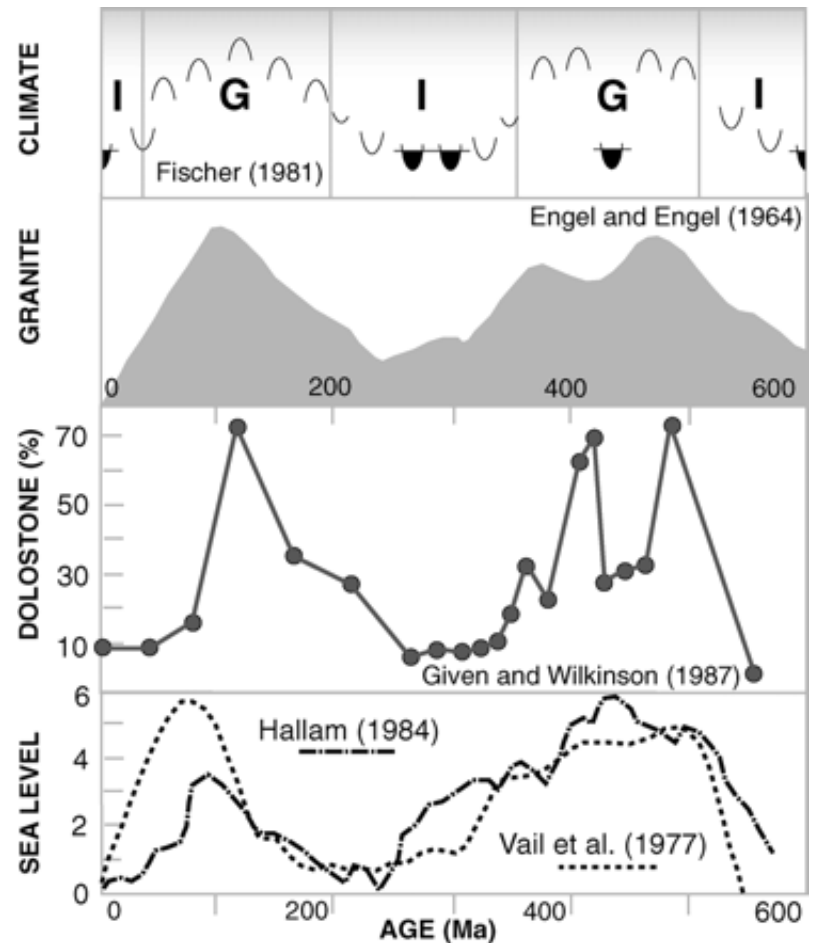
- What are the kinds of changes in the Earth's surface and climate that might affect life?
 - Level of atmospheric oxygen
 - Level of atmospheric carbon dioxide
 - Average global temperature
 - Sea level
 - Number of continents
- Predictions might be that terrestrial diversity would be driven up by high oxygen levels, high (or low?) temperatures, low sea levels, high numbers of continents...
- But note that these can contradict – low sea level might mean more land, but it also means fewer *separate* pieces of land

Major patterns through time 2

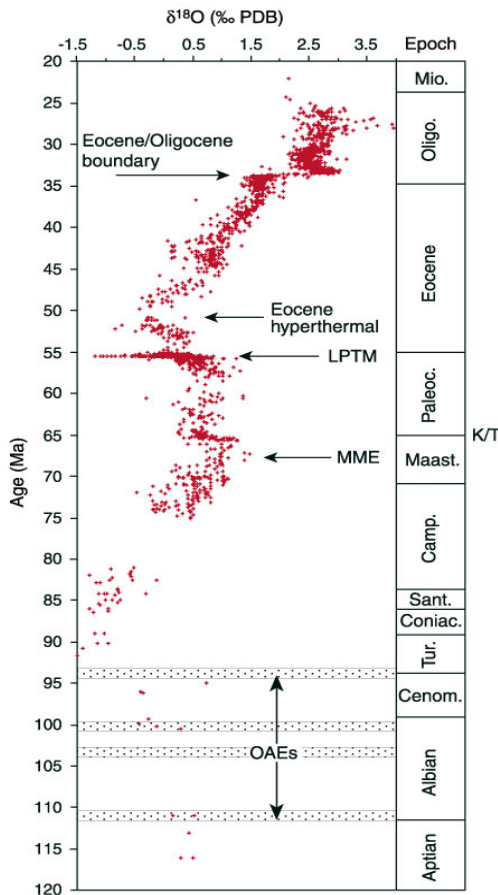


Long-term climate change in the past 600 Myr

- Climate has varied enormously through geological time
- Long-term 'supercycles' of 150 Myr duration
- Repetitions of Greenhouse (G) and Icehouse (I) conditions – we're currently in I; early Palaeozoic and Mesozoic were G
- Perhaps driven by internal dynamics of the Earth – e.g. in mid Cretaceous (100 Mya), a massive increase in MOR activity -> sea level rise -> T rise



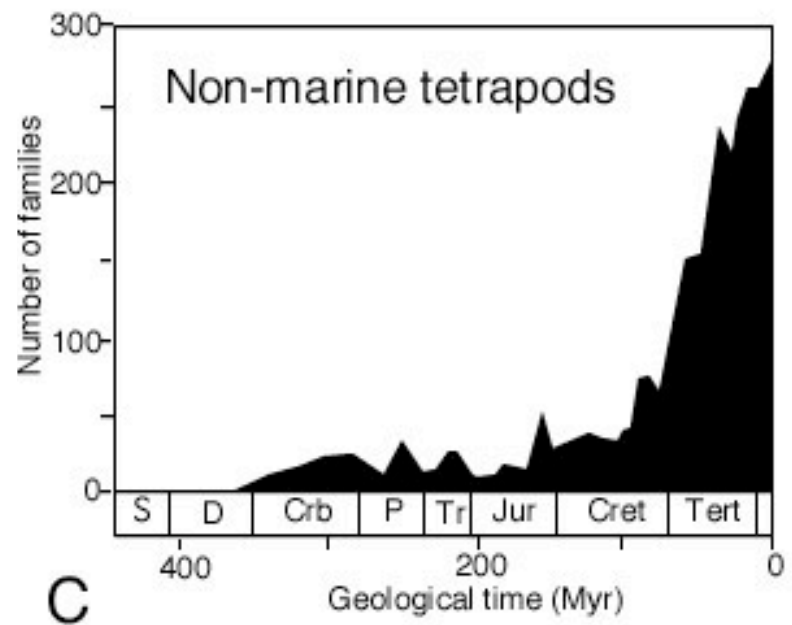
Cooling climates in the past 100 Myr



- Oxygen isotopes show patterns of temperature change; warm to left, cool to right
- Long-term cooling trend since the mid-Cretaceous, 90 Mya, following higher temperatures through earlier parts of Mesozoic
- A number of sudden temperature change events have been identified:
 - Mid-Maastrichtian Event (MME), cooling
 - Late Paleocene Thermal Maximum (LPTM)
 - Eocene hyperthermal, cooling
 - Eocene-Oligocene boundary, warming

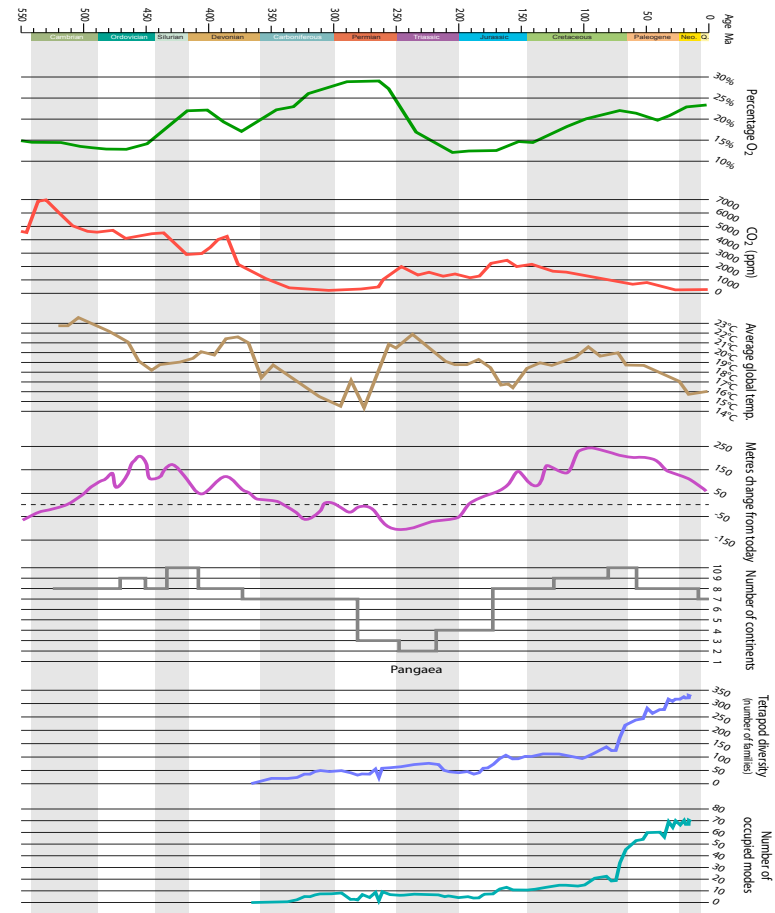
Drivers of diversification 1

- Why did tetrapods (and presumably other groups) diversify? Three possible explanations:
 1. increasing regional-scale endemism as the continents broke up through the past 200 Myr (or climate change)
 2. increasing occupation of terrestrial ecospace
 3. increasing specialization
- Let's assess these three



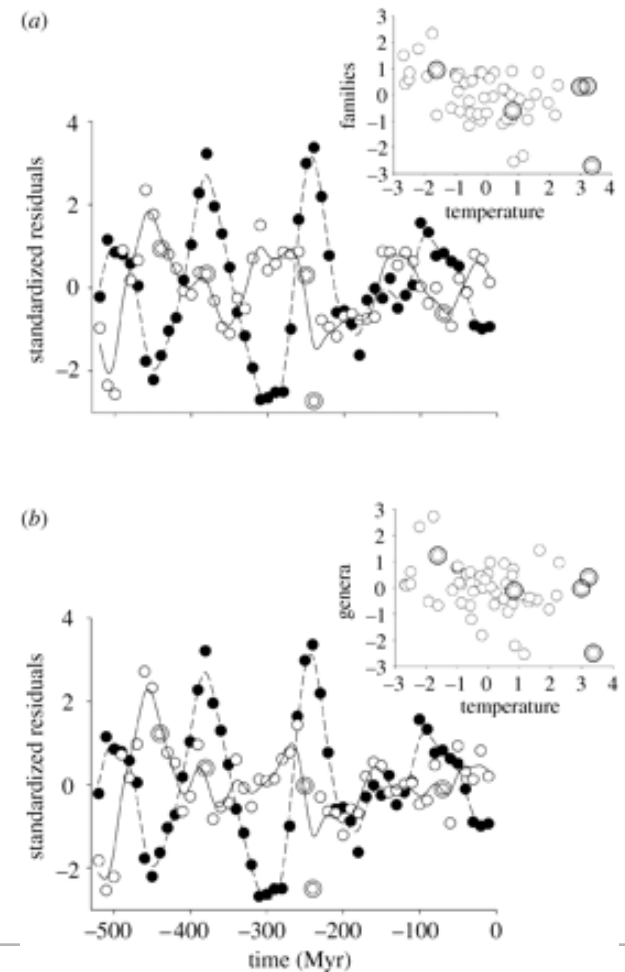
Drivers of diversification 2

- It isn't number of continents, because NOC *declines* as diversity rises
- Further, it doesn't seem to be atmospheric oxygen, carbon dioxide – as diversity rocketed, these measures changed only modestly
- Long-term decline in global temperature since the mid Cretaceous does seem to match the rise in tetrapod diversity



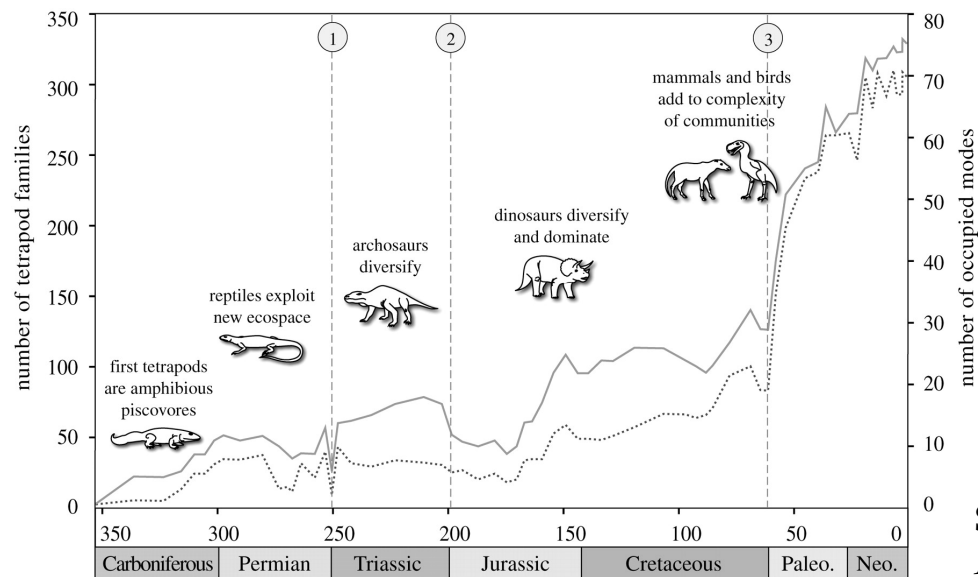
Drivers of diversification 3

- Mayhew *et al.* (2007, *PRSB*) argued strongly that mean global temperature (T) was a major driver of diversity (D) on land and in the sea
- They found, for families (top) and genera (below) that high T (high CO₂, black dots) corresponded to low D (open dots) – turnover was high, but overall D low in greenhouse phases
- Pattern seems to be out of phase by 30 Myr, but it's not just the last 120 Myr



Drivers of diversification 4

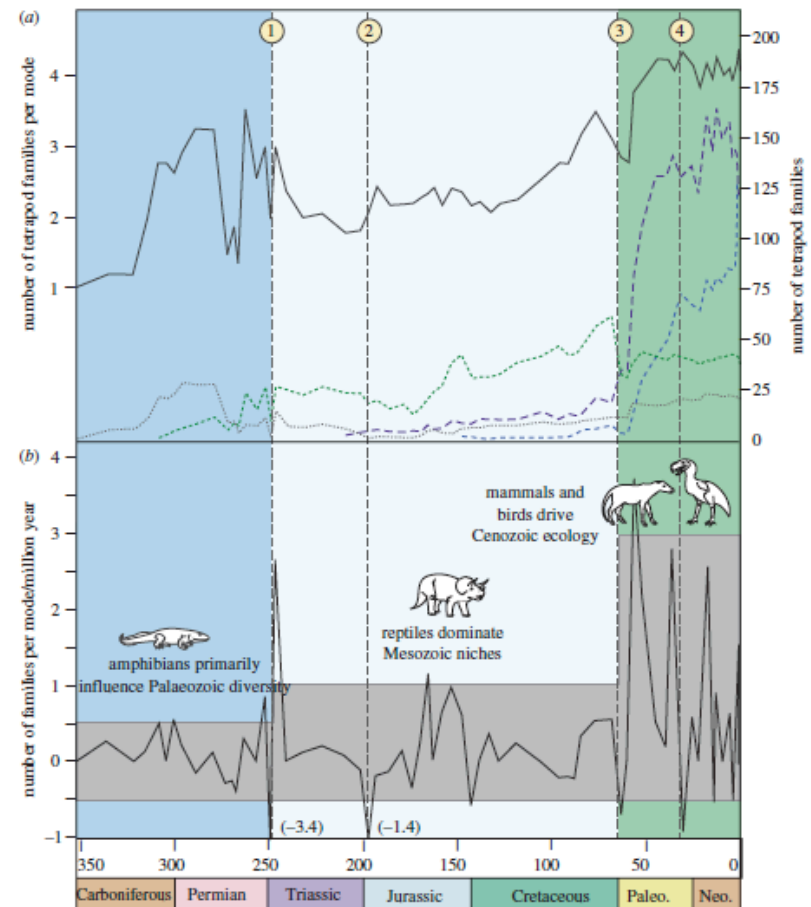
- Number of ecological modes (lower line) is closely tracked by family diversity (upper line) – 1034 tetrapod families in 75 modes
- Suggests that a major driver of diversification has been conquest of new ecospace



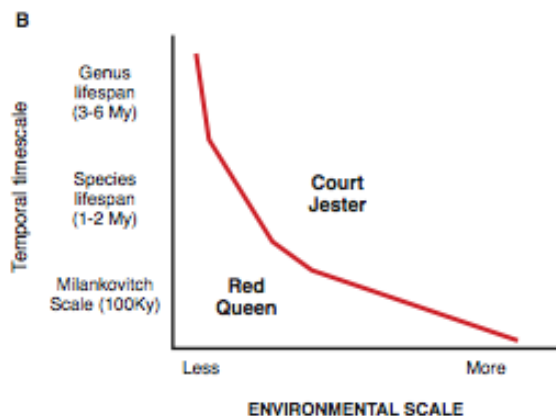
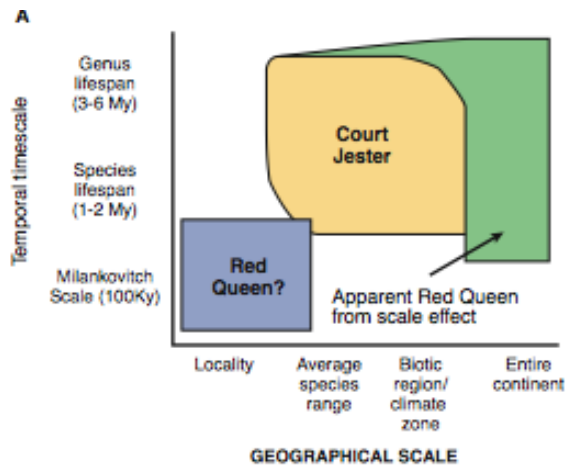
Sahney *et al.* 2010,
Biology Letters

Drivers of diversification 5

- Ecological modes (3 size x 16 diet x 6 habitat) = 288, of which 207 are feasible, and 75 are occupied
- Most new tetrapod bauplans (= families) arose by **entering new ecospace** or new geographical areas
- **Specialization** may then have a role *within* families, as species divide up food and other resources
- Perhaps biodiversity is accounted for by exploitation of new ecospace, with a smaller role for specialization



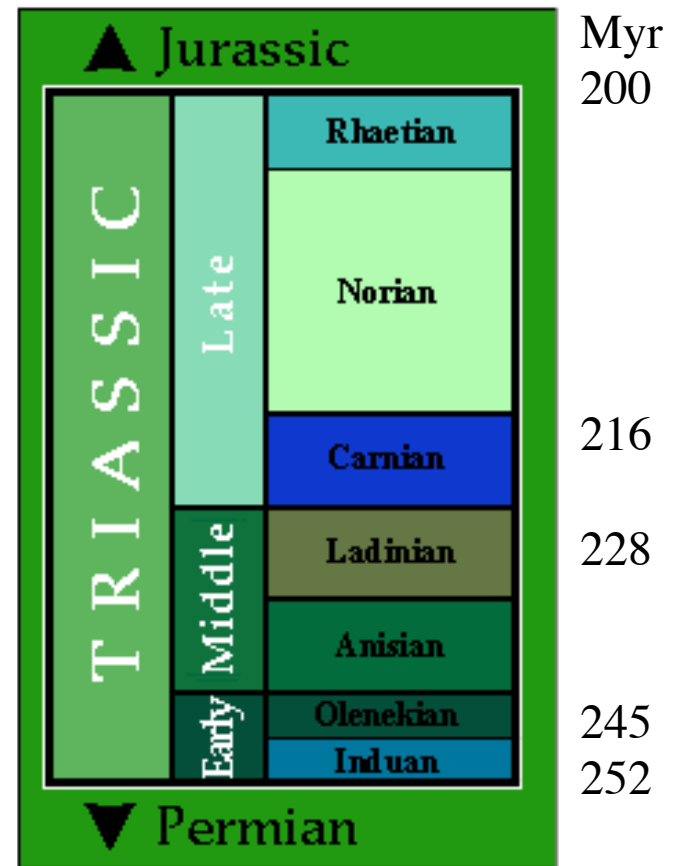
Biotic vs. abiotic factors?



- The ‘Red Queen vs. the Court Jester’ (Barnosky 2000, *JVP*; Benton 2009, *Science*)
- Darwinian evolution (competition, speciation) is the key at ecological scales (species, years to thousands of years)
- Larger events punctuate or re-set these normal phases of evolution – expansion into a new habitat, sudden crisis, sustained temperature change
- So biodiversity is a complex amalgam of large-scale (bauplan/family) processes and ecological scale (Red Queen) processes
- Consider a case study

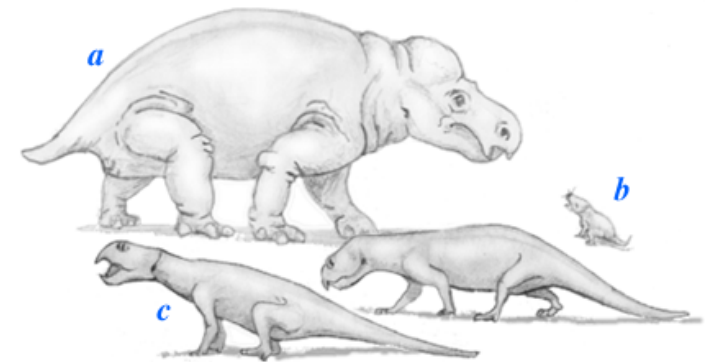
Origin of the dinosaurs 1

- During the Triassic Period there was a replacement of basal reptiles (synapsids, rhynchosaur, crurotarsans) by dinosaurs
- The oldest dinosaurs are Carnian, and dinosaurs radiated in the Norian
- Did the group expand and succeed by competition with their precursors, or did they expand opportunistically, without major competition?
- If the latter, what triggered it? Climate change?

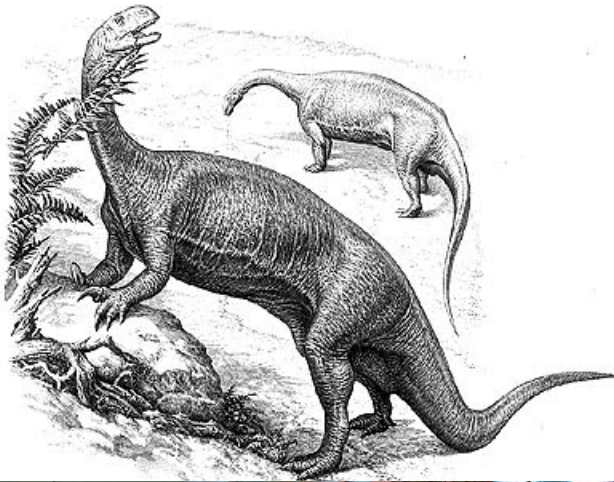


Origin of the dinosaurs 2

- Key herbivores:
 - Synapsids
 - Rhynchosaurs
 - Dinosaurs
- Key carnivores
 - Crurotarsans
 - Dinosaurs



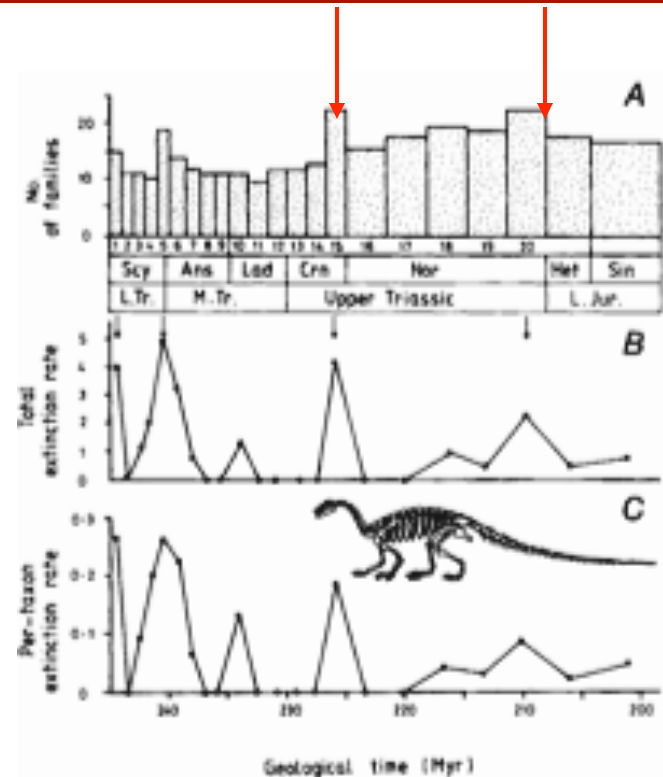
Origin of the dinosaurs 3



- Dicynodonts, synapsid herbivores, and rynchosaurs died out at the end of the Carnian (216 Ma)
- Dinosaurs radiated in the Norian, especially prosauropods like *Plateosaurus*
- Key predators were still crurotarsans
- Then crurotarsans died out at TJ boundary (200 Ma), and new dinosaur clades arose (large carnivores, armoured herbivores)

Origin of the dinosaurs 4

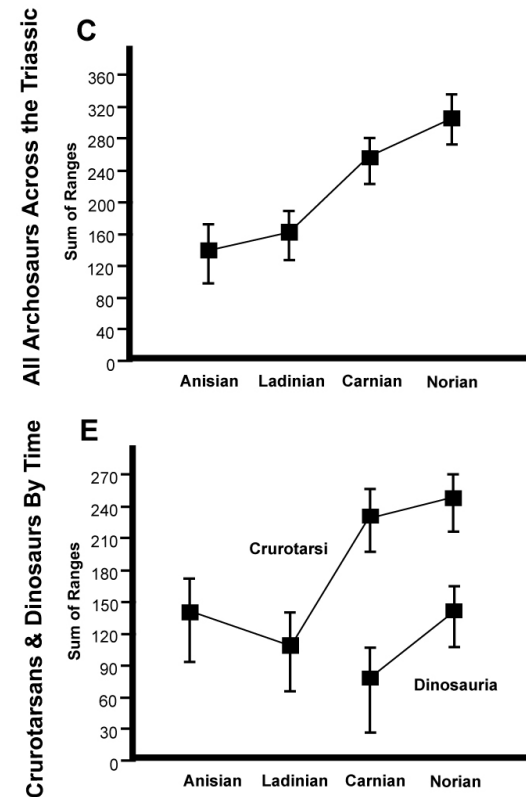
- Taxic counts of apparent generic diversity through the Triassic showed a double extinction - one at the end of the Carnian, and one at the Triassic-Jurassic boundary
- The end-Carnian extinction, or turnover, corresponds to the extinction of only a few families, but these were key herbivores (rhynchosaurs, dicynodonts)
- At the same time, climates were shifting from pluvial to arid - this affected floras and so affected the key herbivores
- Corresponds to the marine record, where a major turnover in the Carnian affected faunas



Benton, M.J. 1986. More than one event in the late Triassic mass extinction. *Nature* 321, 857-861.

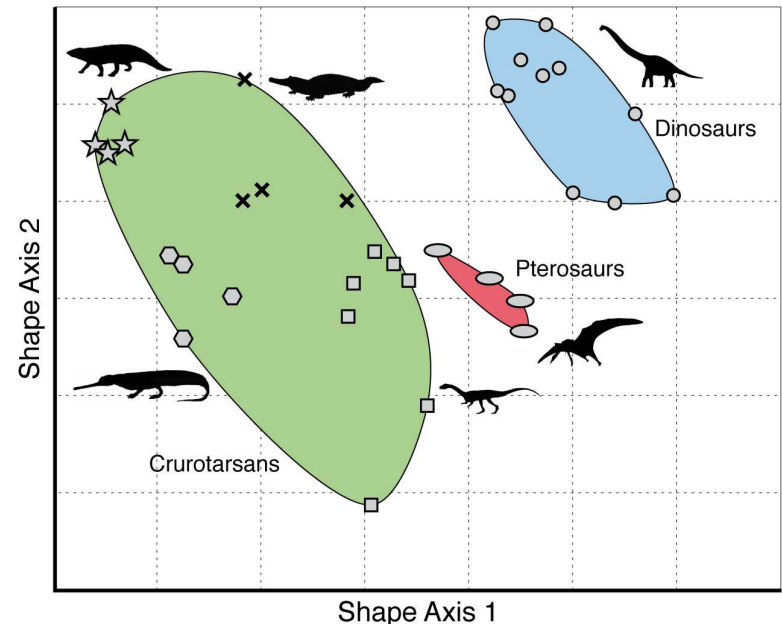
Origin of dinosaurs 5

- A study based on analysis of a data matrix of 64 taxa and 437 characters of skull and skeleton of crurotarsans and dinosaurs
- These were analysed to document rates of change through time, as well as to determine the relative amounts of morphospace occupied
- Archosaurs as a whole show increasing disparity through the Triassic (in line with their diversification after the PT mass extinction)
- Crurotarsi and Dinosauria show the same rise, but Crurotarsi keep ahead of Dinosauria



Origin of dinosaurs 6

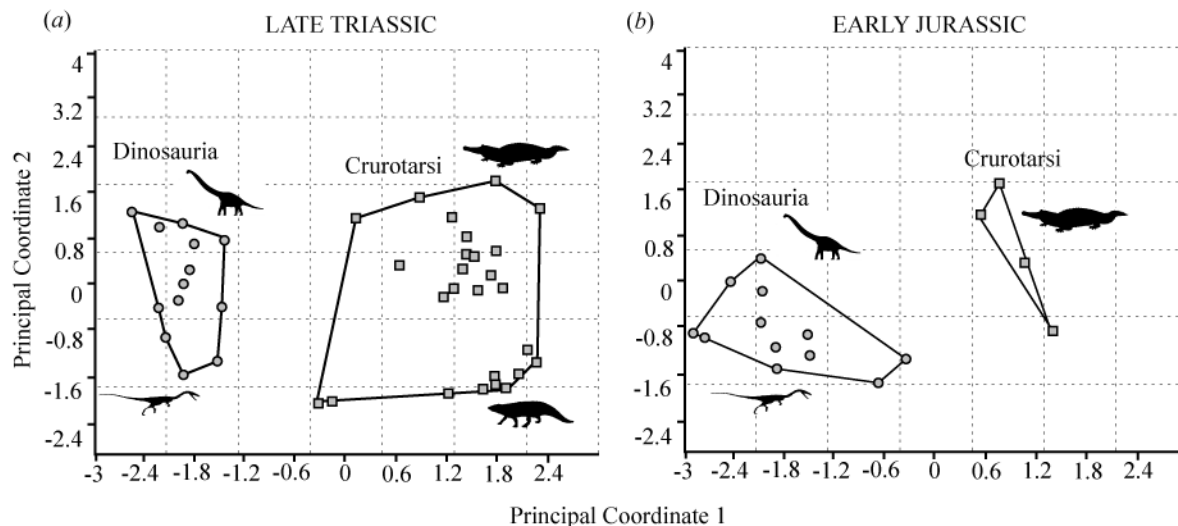
- Numerical assessment of **disparity** shows that dinosaurs occupied a distinct, but small character space in the Late Triassic
- So, dinosaurs did not make enormous headway in the 25 Myr of the Norian - they did a few things (herbivorous prosauropods; small theropods)
- Crurotarsans - their supposed 'inferior' competitors held their diverse array of adaptations throughout the first major phase of dinosaurian evolution



Brusatte, S. L., Benton, M. J., Ruta, M., and Lloyd, G. T. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science*, 321, 1485-1488.

Origin of dinosaurs 7

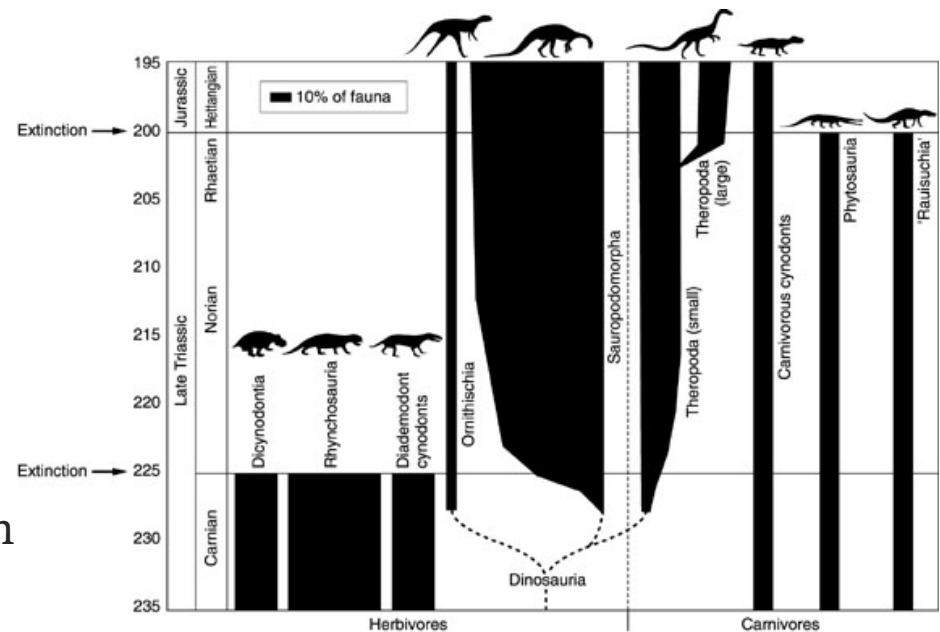
- In a further study, we wanted to look at what happened after extinction event 2 - the Tr-J boundary
- With the extinction of most crurotarsans (except crocodylomorphs), Dinosauria might have taken a leap in morphospace occupation...but they did not



Brusatte, S. L., Benton, M. J., Ruta, M., and Lloyd, G. T. 2008. The first 50 Myr of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology Letters*, 4, 733-736 (October 2008).

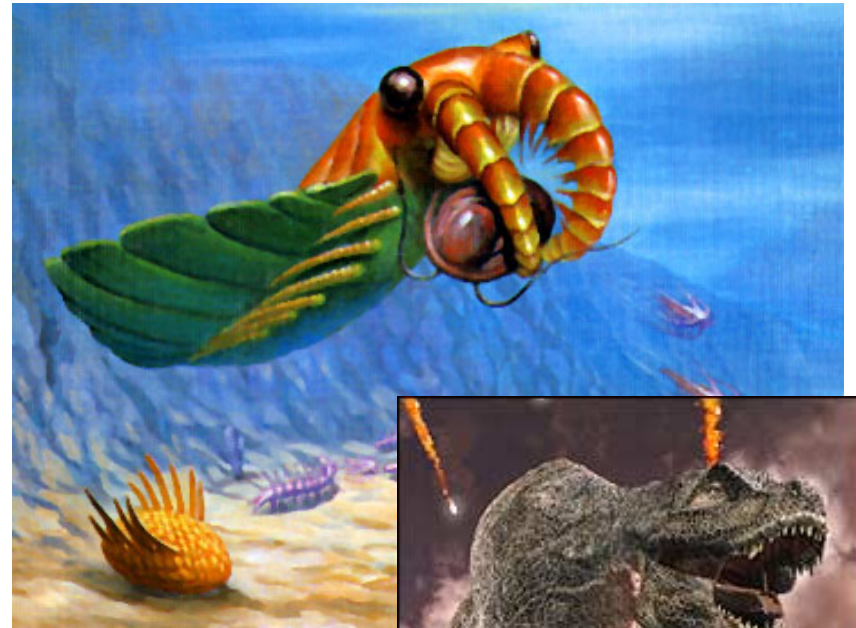
Origin of dinosaurs 8

- The initial expansion of Dinosauria was apparently mediated by two extinction events
 - Extinction 1, triggered by climate change, emptied herbivore ecospace, and prosauropods radiated
 - Extinction 2 emptied carnivore and herbivore ecospace, and theropods and ornithischians radiated
- Dinosaur diversity jumped after each extinction event, but disparity did not change greatly, especially not after extinction 2
- This shows decoupling of diversity and disparity



Diversifications

- Many phases of biodiversity increase (e.g. Cambrian Explosion; rise of mammals) followed crises or major environmental changes
- Study of tetrapods through time showed most new genera and families were associated with occupation of new ecospace
- So macroevolution driven by opportunism and the external environment, not simply a scaling-up of intraspecies competition and specialization



Summary

1. Life has expanded from one species to 10M or more
2. Much of that expansion happened in the last 125 Myr, following the Cretaceous Terrestrial Revolution - this is unlikely to be an artefact of a poor fossil record
3. Falling global temperatures may have had a role in driving up diversity steadily over the past 100 Myr
4. Changes in physical environments constantly affect biodiversity and evolution (e.g. end-Permian mass extinction; Late Triassic aridification; mid-Cretaceous greenhouse phase and KTR)
5. Life has a tendency to expand, and so biodiversity increase has been mainly opportunistic, reflecting the conquest of new ecospace; effectively an escape from competition