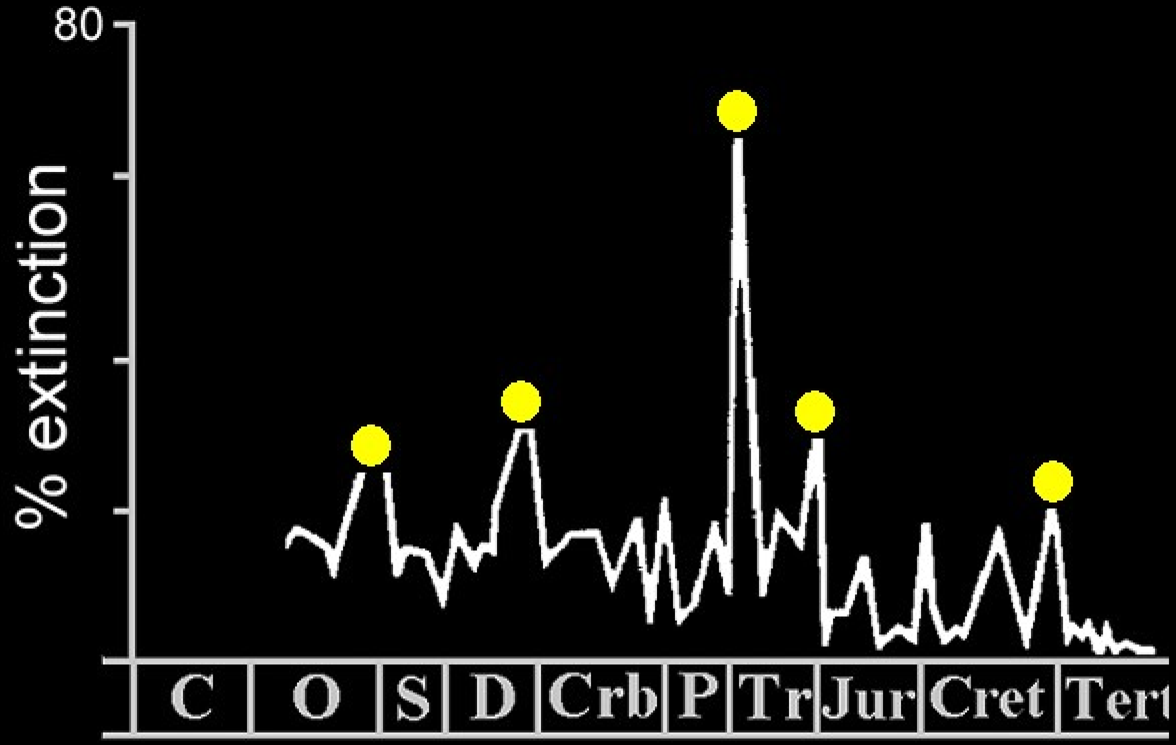
Beyond the "Big Five"

Extinctions as Experiments in the History of Life

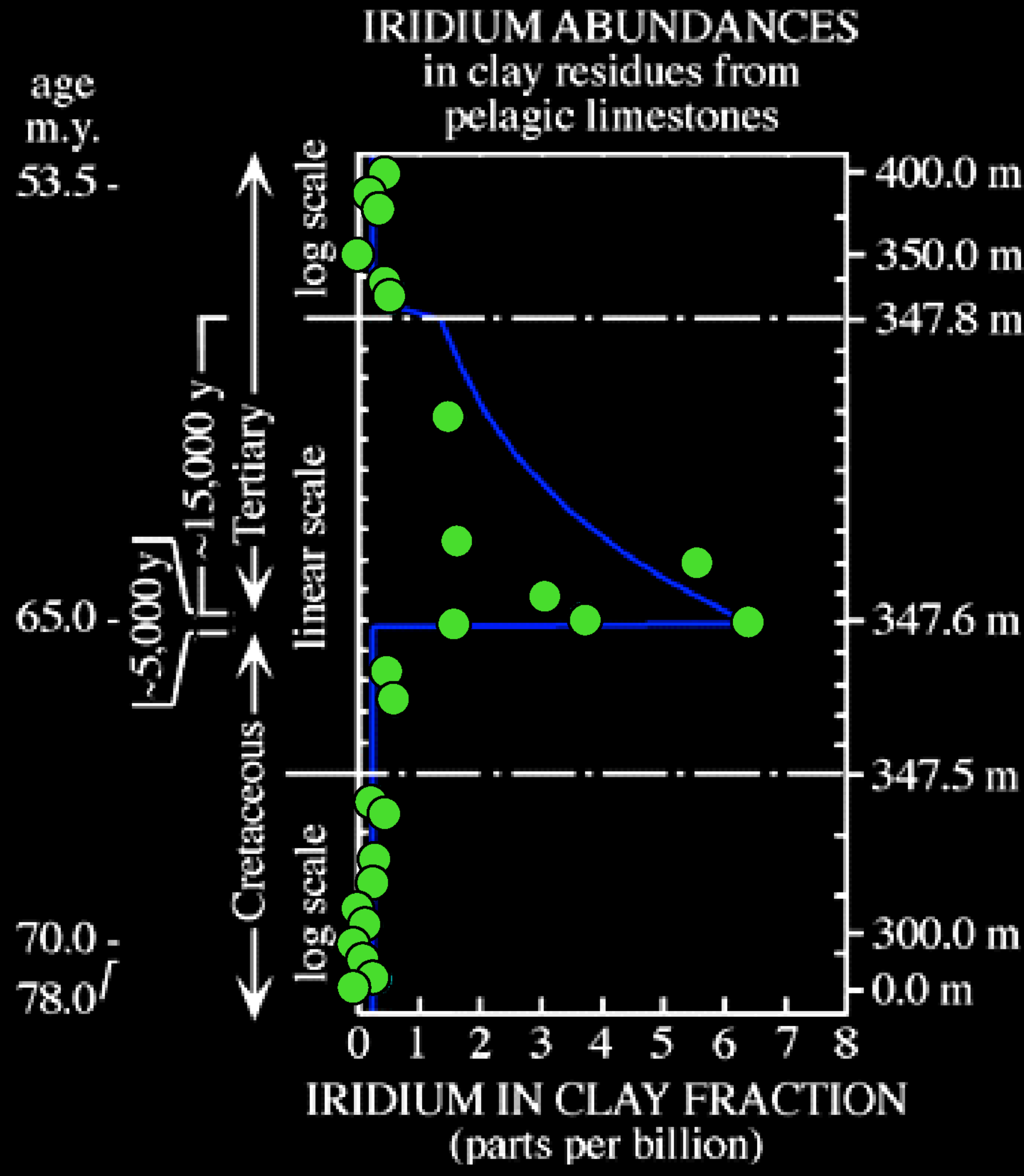


Rowan Lockwood

The College of William and Mary

Breakthroughs in Extinction

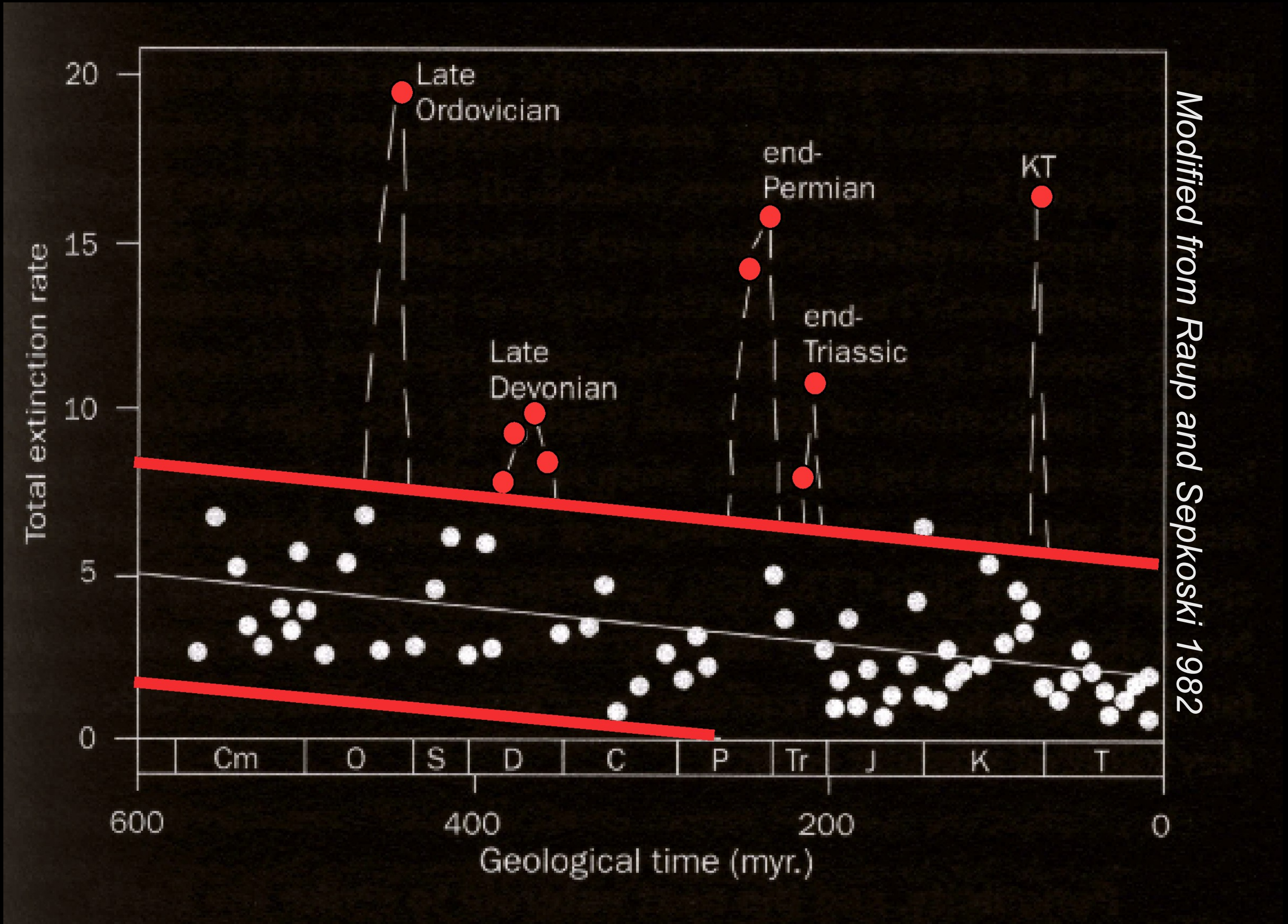
- Alvarez et al. (1980) hypothesis that an ET event was responsible for the K/T extinction



Modified from Alvarez et al. 1980

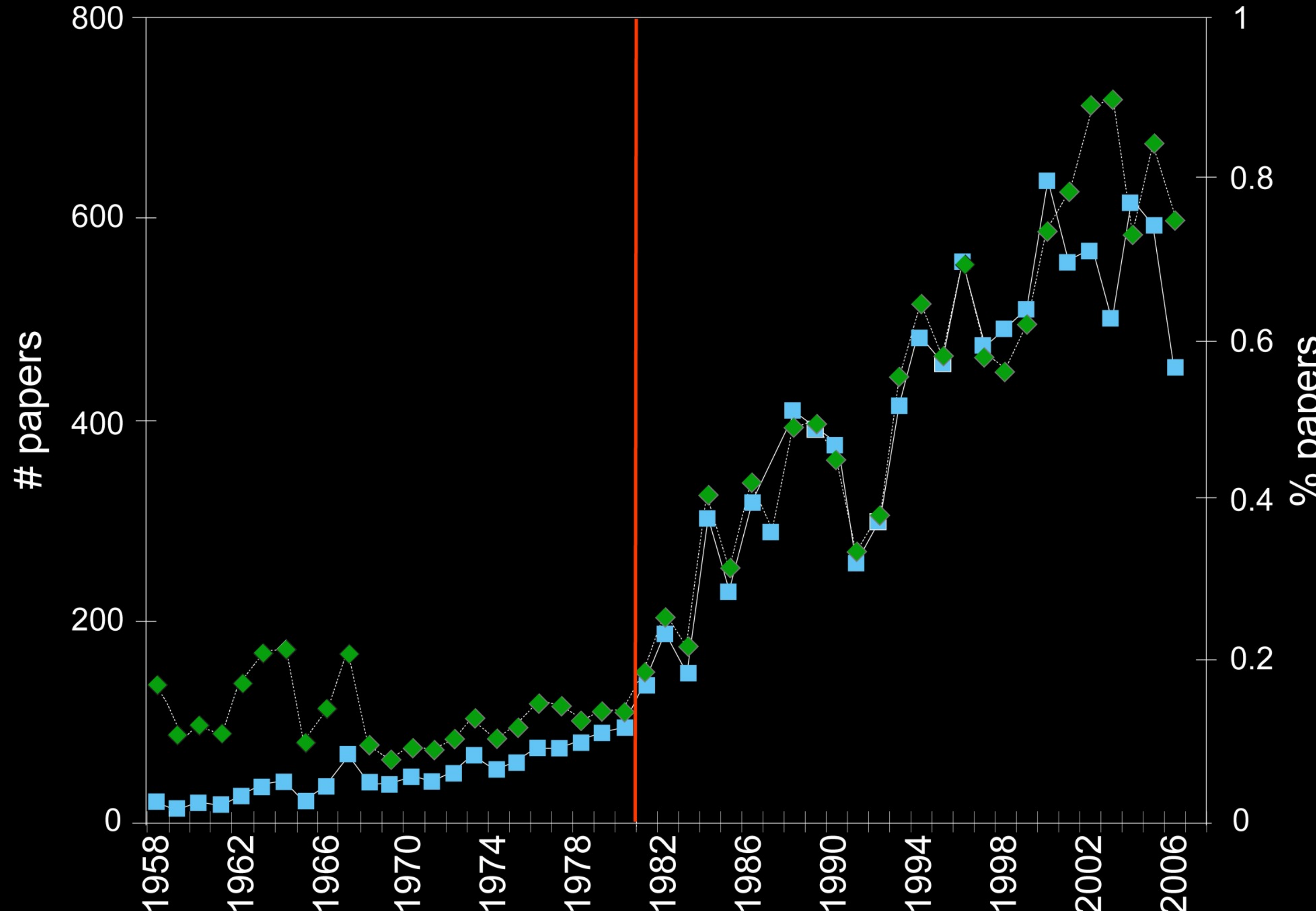
Breakthroughs in Extinction

- Identification of the "Big 5" by Raup and Sepkoski (1982)



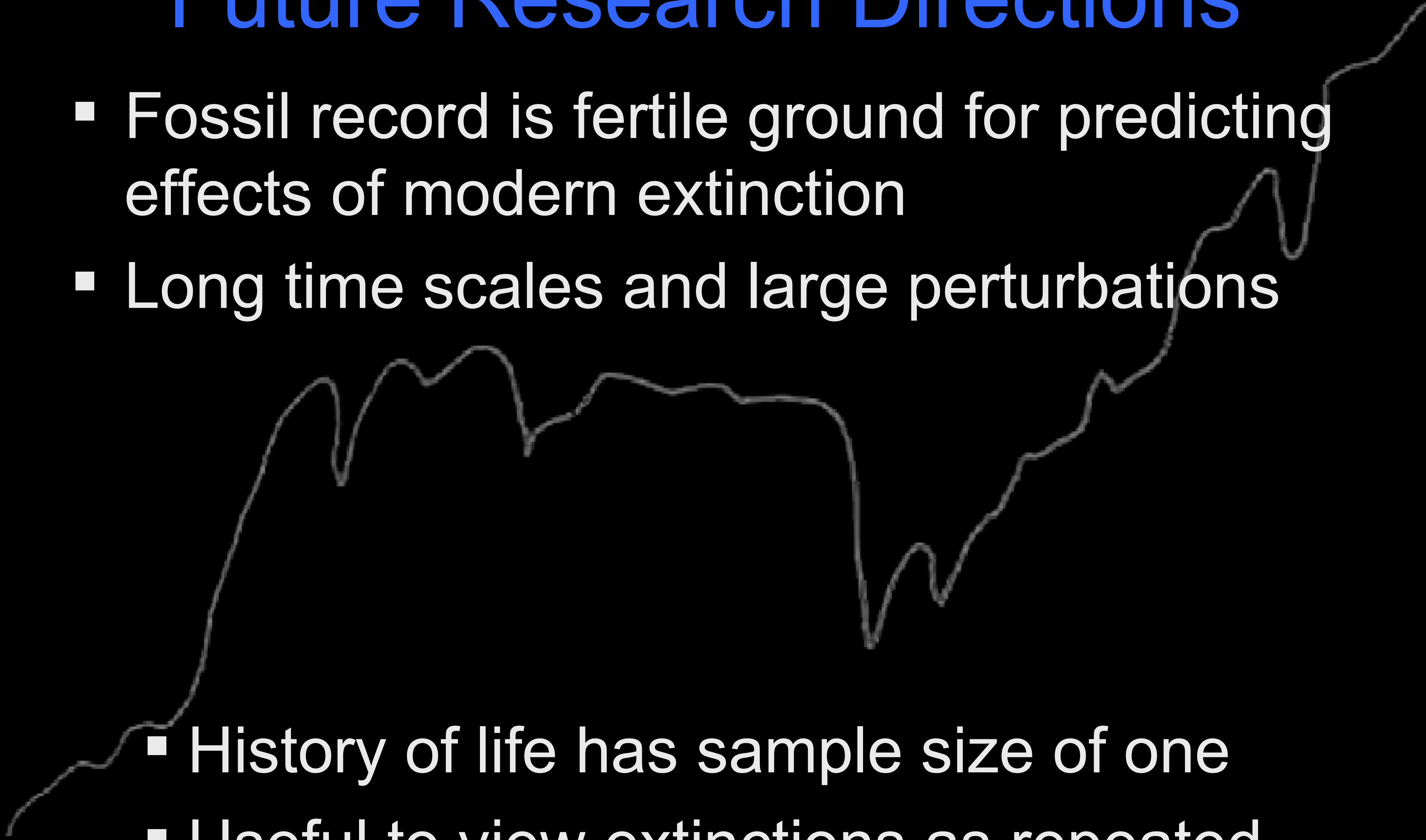
“Extinction Industry”

Handful of papers published in the 1950’s to 1% of all geology papers in 2002



Future Research Directions

- Fossil record is fertile ground for predicting effects of modern extinction
- Long time scales and large perturbations



- History of life has sample size of one
- Useful to view extinctions as repeated natural experiments in the history of life

Future Research Directions

- Will highlight a number of promising research directions
- Exploring a central theme— evolutionary consequences of extinction
- Focusing on three broad areas

    1. Effects of selectivity
    2. Importance of recovery intervals
    3. Influence of spatial patterns

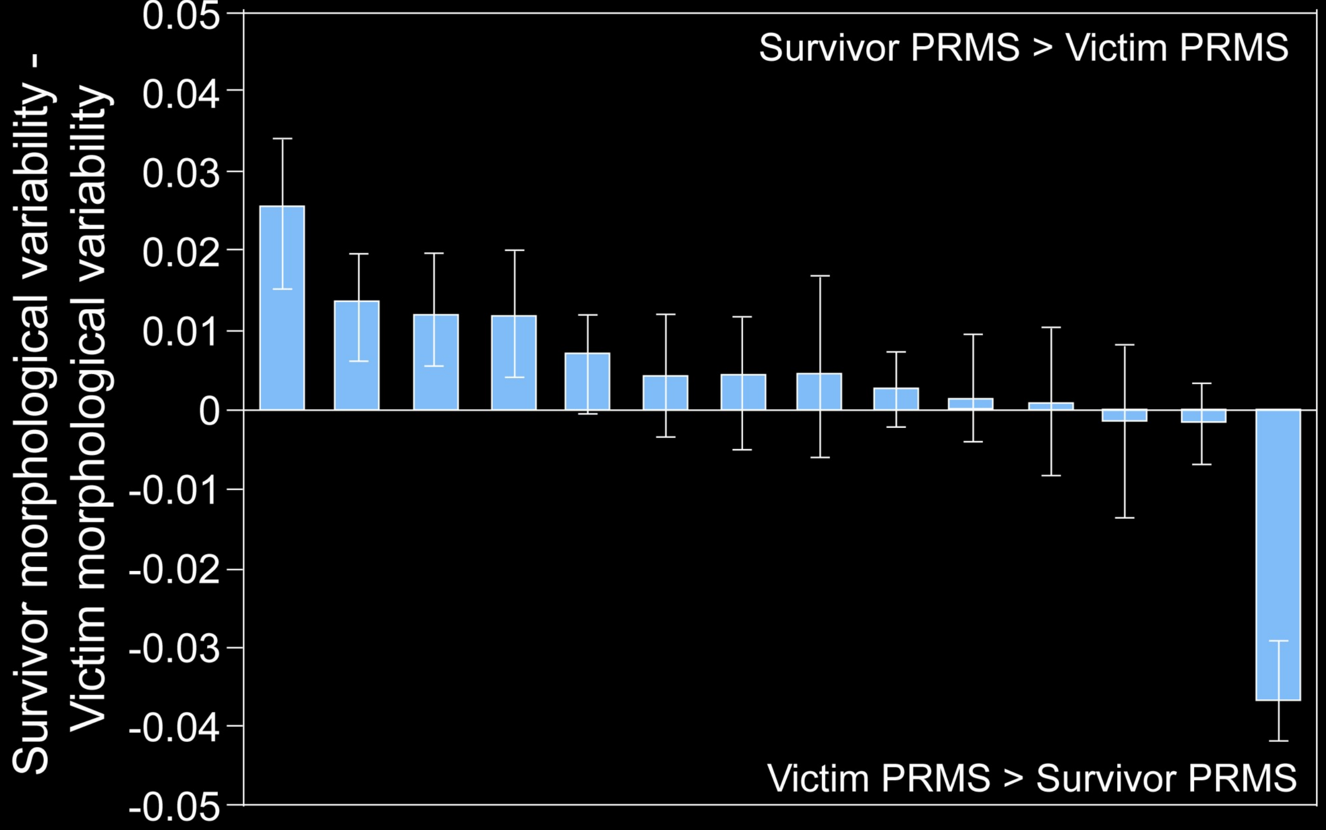
Effects of Selectivity

- Extinctions
  - Eliminate dominant and allow subordinate taxa to diversify
  - Redirect evo trends by eliminating innovations
  - Limit potential evolution by reducing variability

- Many of these mechanisms operate via selectivity

Selectivity: Trait Variation

- Majority of studies focus on mean or dominant traits
- Ignores trait variation-- prereq for evolution



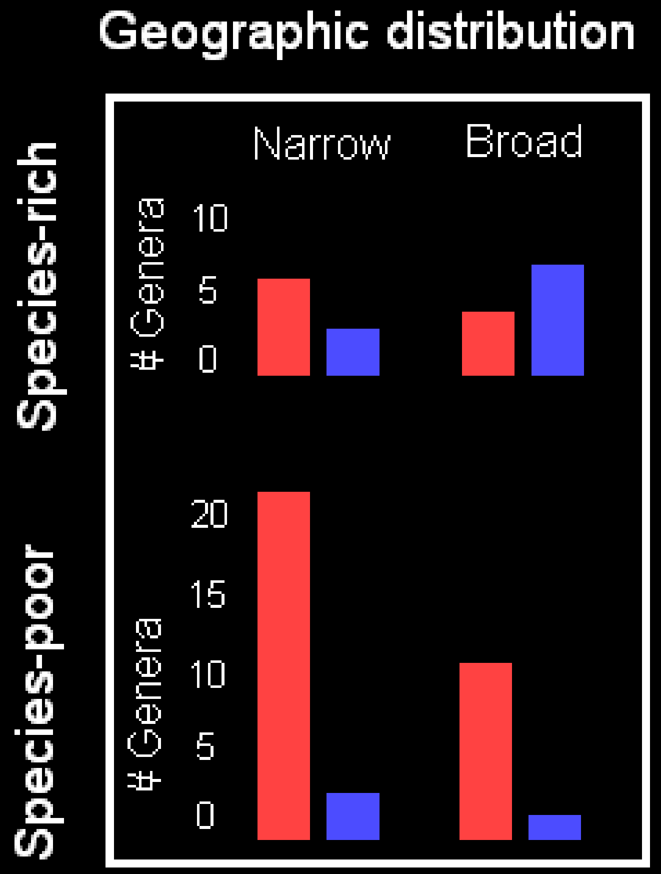
Modified from Kolbe et al. 2006

Selectivity: Multivariate Approaches

- Traditional approach- independent testing of traits
- Biological traits linked to one another-- which traits are actually selected for?

Tools include regression, path analysis, structural equation modeling

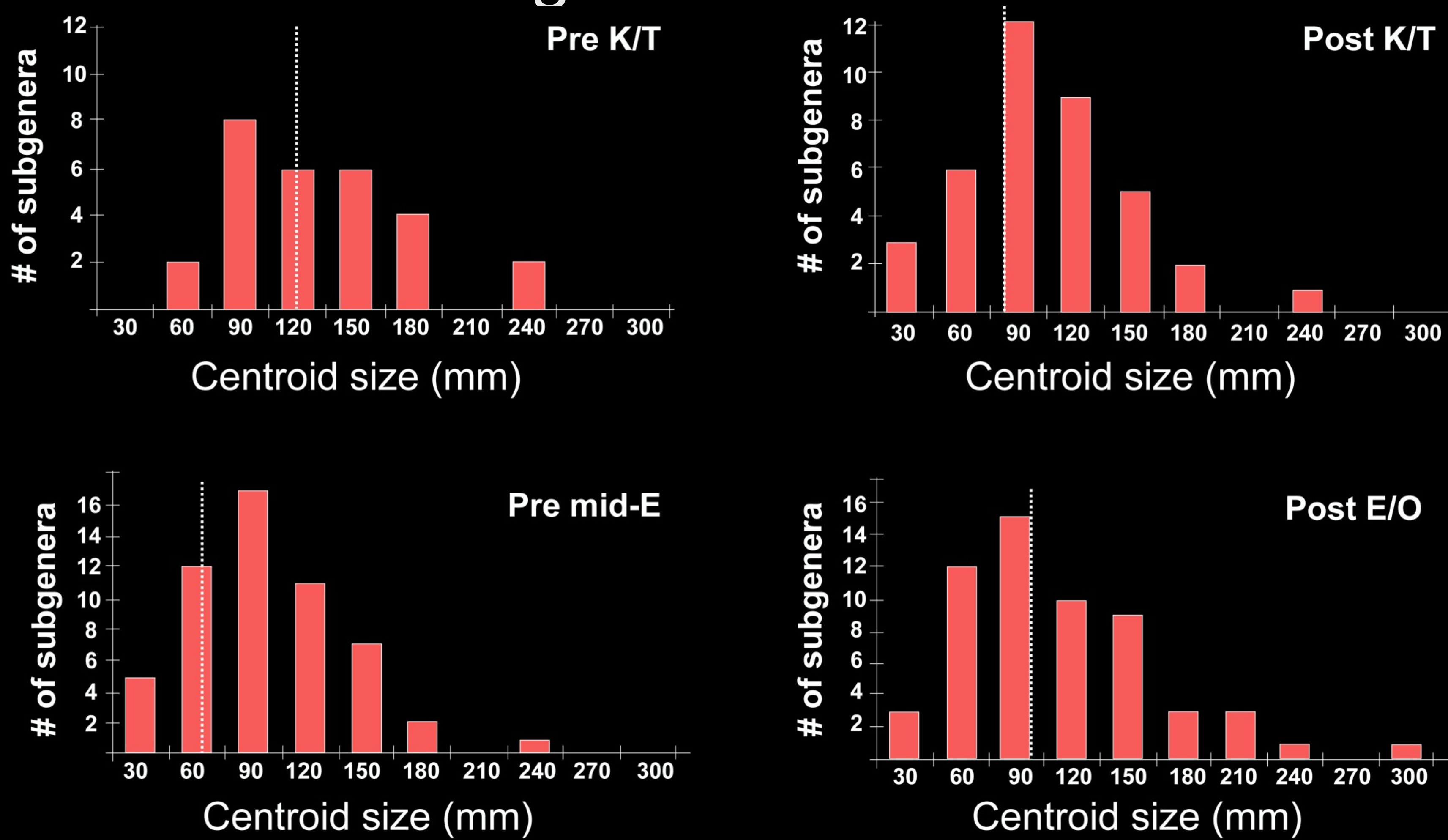
e.g., Harnik 2007, Payne & Finnegan 2007, Jablonski 2008



Modified from Erwin 1989

Selectivity: Background Extinction

- How does selectivity vary across extinctions of different magnitudes and durations?



Modified from Lockwood 2005

Selectivity: Meta-analyses

- Several authors have provided reviews of the selectivity across events and taxonomic levels
- Missing a quantitative, meta-analytical approach to this often contradictory literature
- Recently applied successfully to live-dead studies and species-energy relationships

End-Ordovician bivalves	Bretsky 1973
End-Ordovician brachiopods	Sheehan and Coorough 1990; Sheehan et al. 1996; Brenchley et al. 2001; Harper and Rong 2001
End-Ordovician bryozoans	Anstey 1986; Anstey et al. 2003
End-Ordovician trilobites	Robertson et al. 1991
End-Ordovician marine invertebrates	Foote 2003
Late Devonian bivalves	Bretsky 1973*
End-Permian bivalves	Bretsky 1973
End-Permian gastropods	Erwin 1989, 1993, 1996†
End-Triassic bivalves	Bretsky 1973; Hallam 1981; Hallam and Wignall 1997: p. 148‡
End-Cretaceous bivalves and gastropods	Jablonski 1986a,b, 1989; Jablonski and Raup 1995
Exception: End-Cretaceous echinoids	Smith and Jeffery 1998, 2000a,b

* Rode and Lieberman (2004) found broad geographic range to promote species survivorship in the Late Devonian but did not provide genus-level analyses.
† Contrary to Smith and Jeffery's (2000b) misreading of these results.
‡ McRoberts and Newton (1995) report no effect of species-level geographic range on species survivorship for European end-Triassic bivalves, consistent with end-Cretaceous results, but they do not provide genus-level statistics.

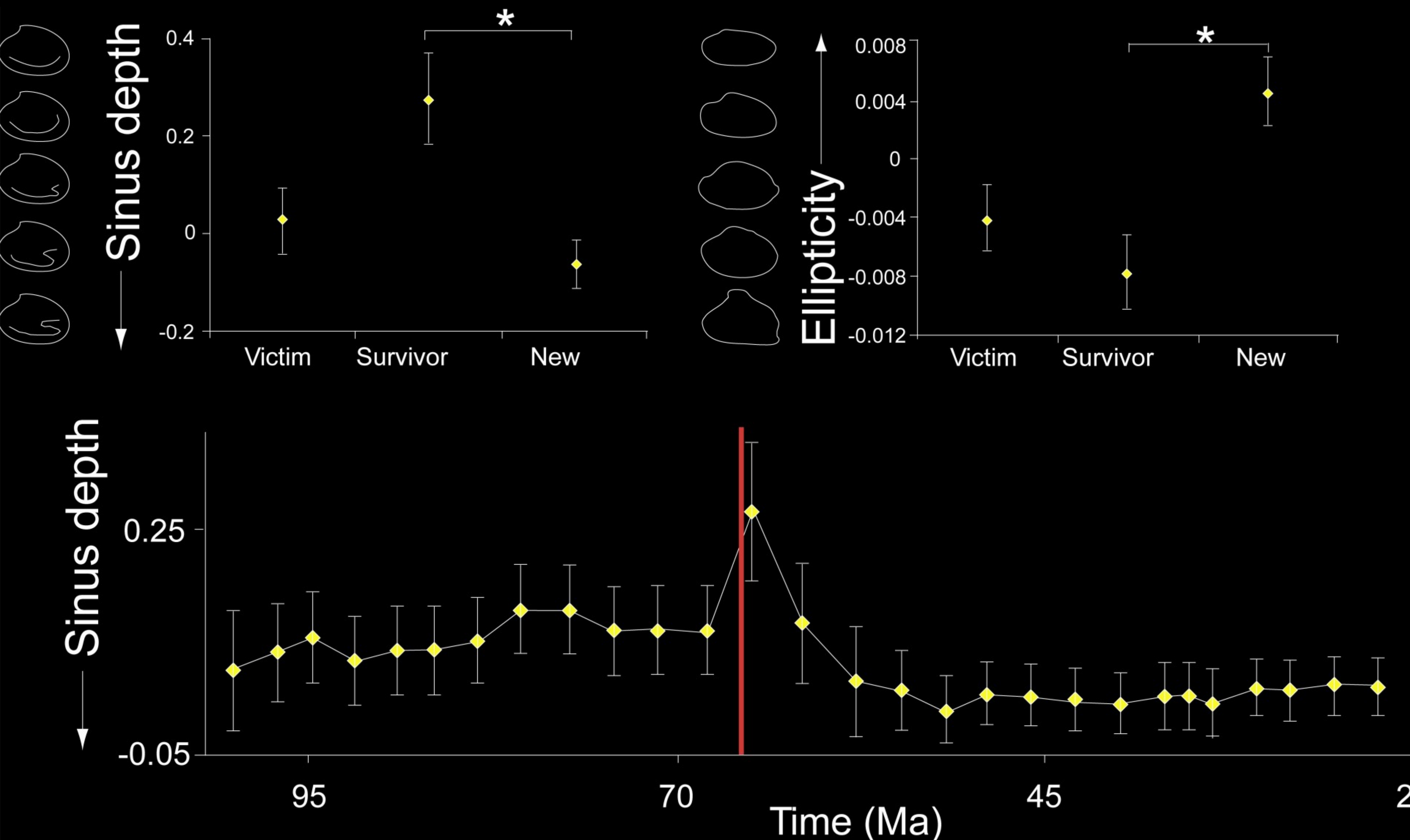
Modified from Jablonski 2005

Importance of Recovery Intervals

- To understand influence of mass extinctions on evolutionary patterns, must examine both extinction and recovery
- Despite recent rise in recovery work, we still know little about recolonization
- Unfortunate given potential parallels between post-extinction recovery and restoration ecology

Recovery: Selectivity

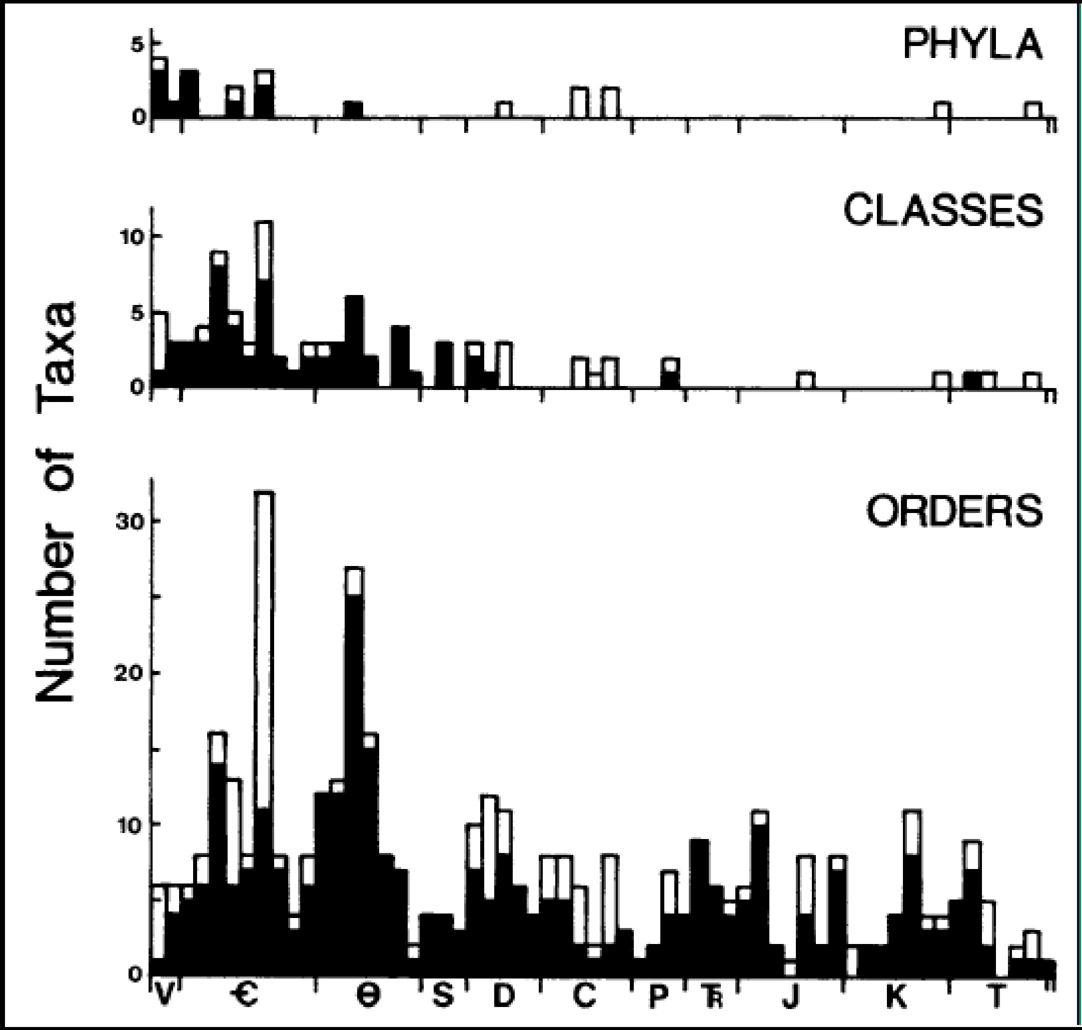
- Evolutionary impact of recovery is closely tied to selectivity; few studies have examined this
- Failure to recover can be just as important as failure to survive
- Prolonged duration of recoveries increases importance to long-term macroevolutionary trends



Modified from Lockwood 2004

Recovery vs. Radiations

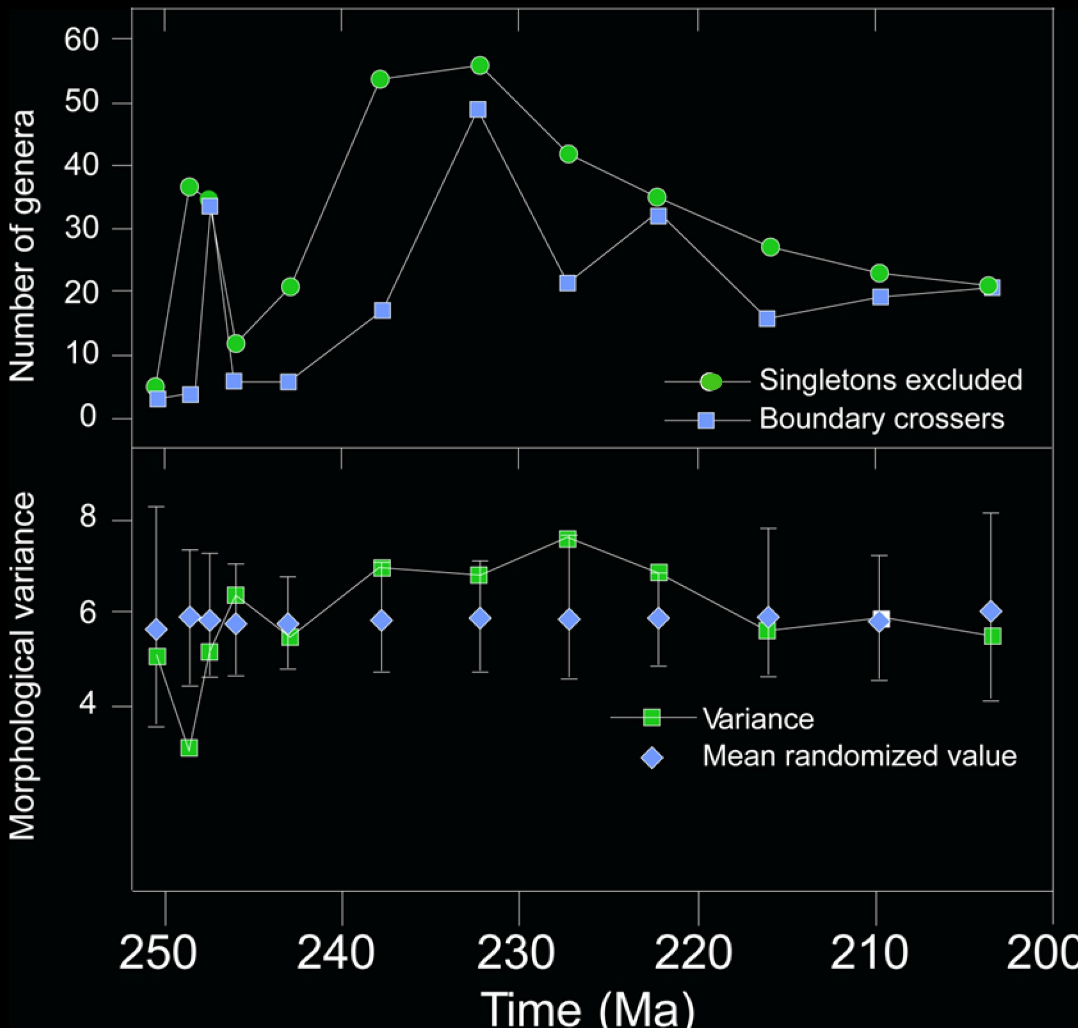
- Repeated nature of extinctions and recoveries allows us to test hypotheses of phylogenetic versus ecological constraint in the early evolution of clades
- e.g., Erwin et al. 1987, Foote 1996, 1999



Modified from Erwin et al. 1987

Recovery: Ecological & Evolutionary trends

- Few studies have assessed how trends, from latitudinal diversity gradients to onshore-offshore patterns of origination, shift across recovery intervals



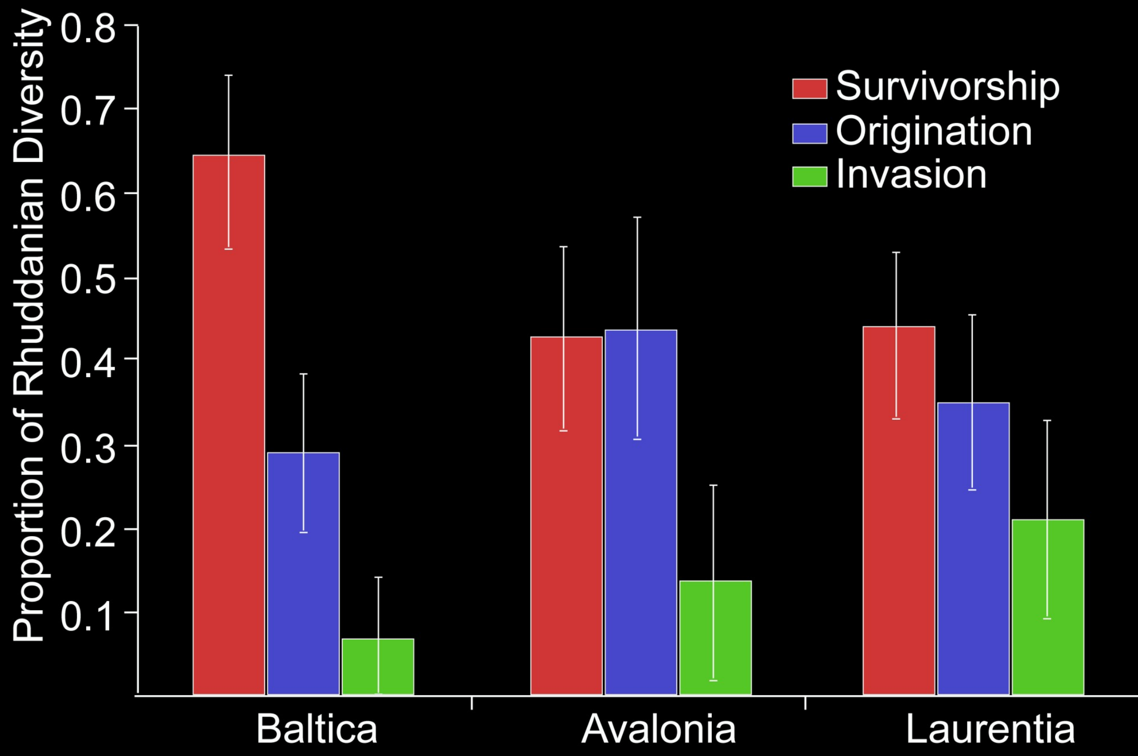
Modified from McGowan 2004

Influence of Spatial Patterns

- Studies of extinction often performed at outcrop or global scale
- Different responses in different regions can be used as controls in natural experiments of extinction
- Environmental factors important in one region may not be in another, allowing us to assess causal mechanisms

Spatial: Extinction vs. Emigration

- Difficult to differentiate extinction and origination from migration
- Regional studies may help predict which ecosystems are likely to experience invasion



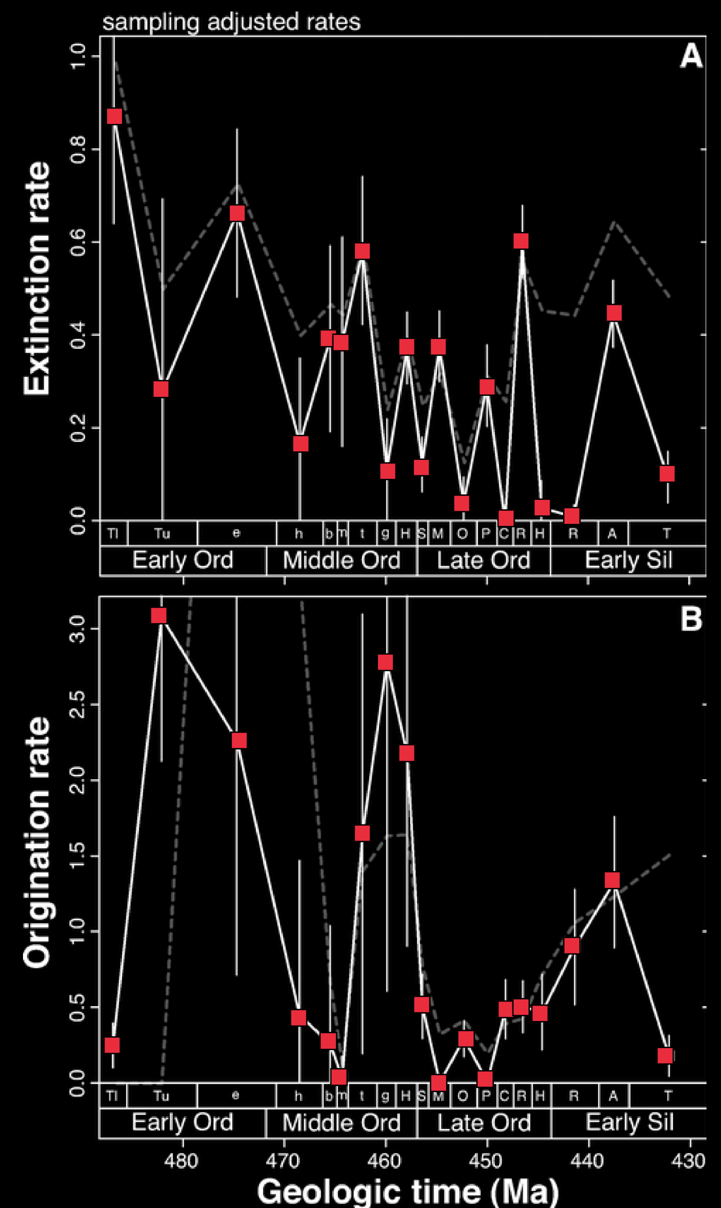
Modified from Krug and Patzkowsky 2007

Spatial Autocorrelation

- Non-independence of samples in space serious problem for extinction studies
- Recognized as a potential bias in ecology
- Can highlight ecologically important mechanisms such as source-sink dynamics
- Handful of studies resample patterns environmentally, but not spatially

Preservation, Sampling, & Other Factors

- Understanding of intrinsic and extrinsic factors that affect extinction metrics
- Intrinsic factors include variable sampling, taxonomic standardization, etc.
- Extrinsic factors include availability of rock record, sequence architecture, etc.
- Recent attempts to control for both yield extremely volatile extinction rates (e.g., Foote 2007; Peters and Ausich 2008)



Modified from Peters and Ausich 2008

Conclusions I

- Past century has witnessed significant breakthroughs in study of extinction in the fossil record

- Future research directions focus on three broad research areas
    1. Effects of selectivity
    2. Importance of recovery intervals
    3. Influence of spatial patterns

Conclusions II

- Topics explored include:
  - Role that trait variation plays in survivorship
  - Comparative effects of extinctions of varying magnitudes on evolutionary patterns
  - Re-establishment of patterns in the aftermath of extinction
  - Extent to which spatial autocorrelation affects extinction patterns
- Useful to view extinctions as repeated natural experiments in the history of life and develop hypotheses to explicitly test across multiple events

Acknowledgments

- R. Bambach and P. Kelley for developing short course
- M. Foote, D. Jablonski, P. Wagner, J. Swaddle, M. Kosnik, P. Kelley, and A. Stigall for useful feedback
- ACS Petroleum Research Fund and the Jeffress Memorial Trust for funding
- Manuscript developed while a Sabbatical Fellow at the NCEAS, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara, and the State of California