Tracking Species in Space and Time:

Assessing the relationships between paleobiogeography, paleoecology, and macroevolution

Alycia L. Stigall

Department of Geological Sciences and
OHIO Center for Ecology and Evolutionary Studies

1804 OHIO UNIVERSITY

Outline

New methods and emerging opportunities in paleobiogeography:

- Biogeographic controls on macroevolution
- Biogeographic range and paleoecology/extinction
- Potential for synthesis

Case Studies:

- Miocene Radiation of Equinae
- Late Devonian Biodiversity Crisis
- Late Ordovician Richmondian Invasion

Future research directions

Controls on species range

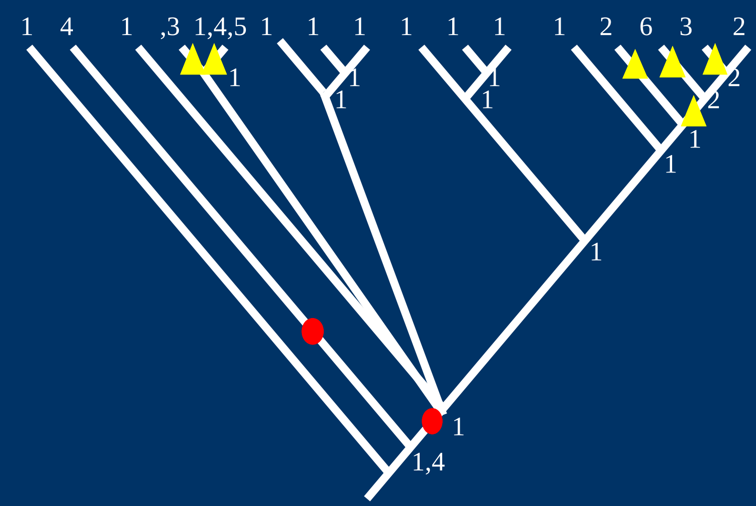
Historical Factors

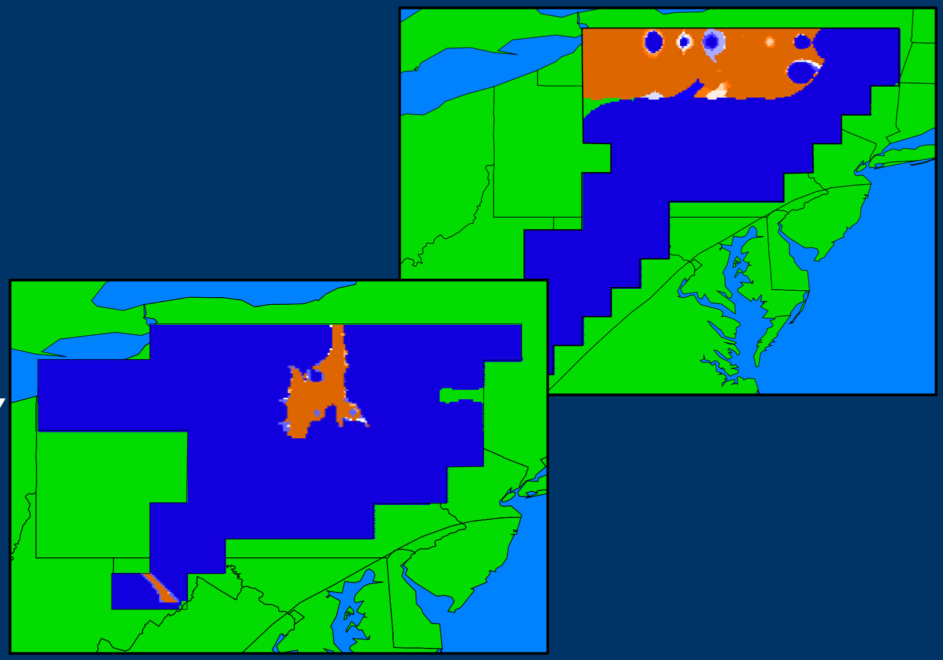
- Primary during speciation

Ecological Factors

- Primary during species duration & extinction

- Traditionally separate subdiciplines
    - *Historical Biogeography*
    - *Ecological Biogeography*

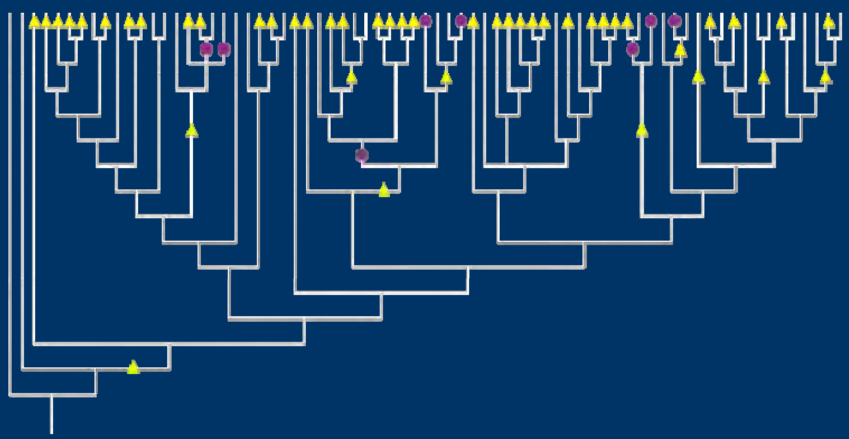




Integrated biogeographic approach, part I

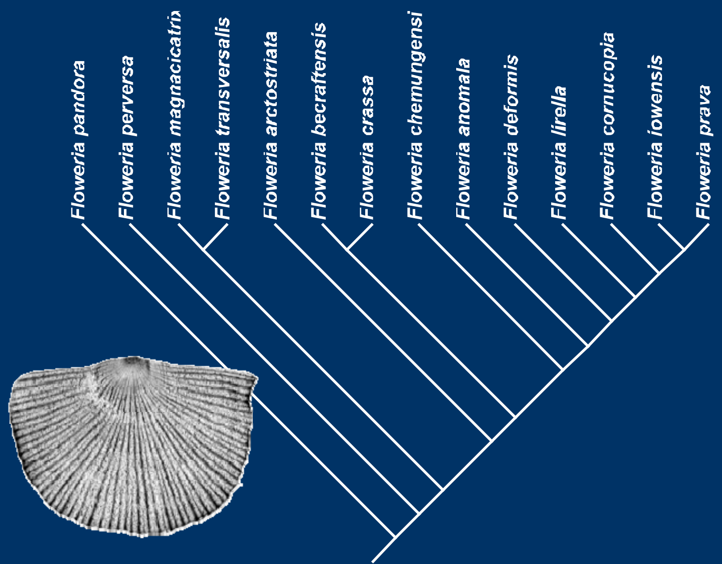
Relationship between biogeography & macroevolution

- Research questions:
  - Speciation mode
  - Clade history
  - Adaptive radiations
  - Tectonic vs climatic influences
- Tools: phylogenetic biogeography (detailed in Lieberman, 2000)

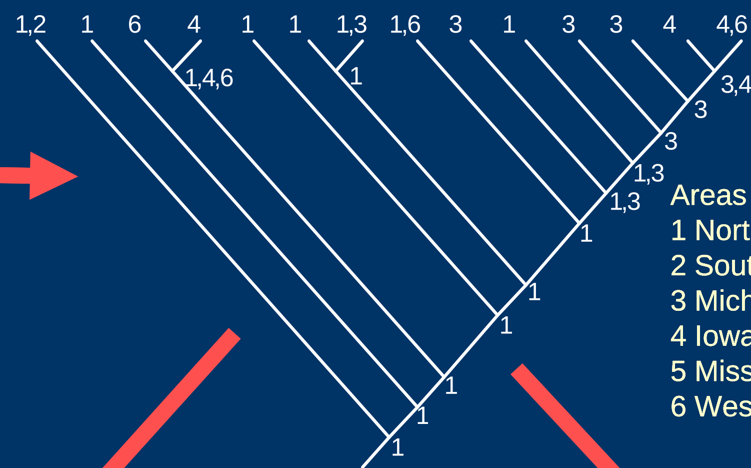


Phylogenetic biogeography

Evolutionary relationships

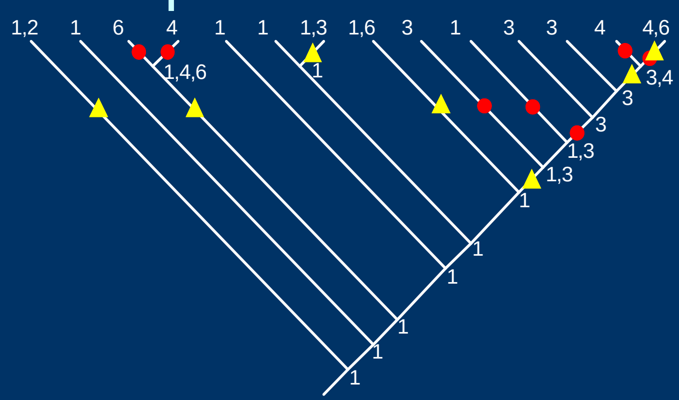


Evolution of biogeographic areas

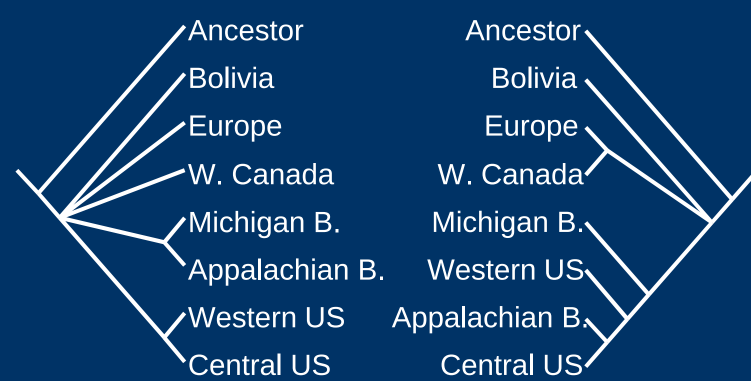


Areas of Endemism:
1 Northern Appalachian basin
2 Southern Appalachian basin
3 Michigan Basin
4 Iowa Basin
5 Missouri Basin
6 Western United States

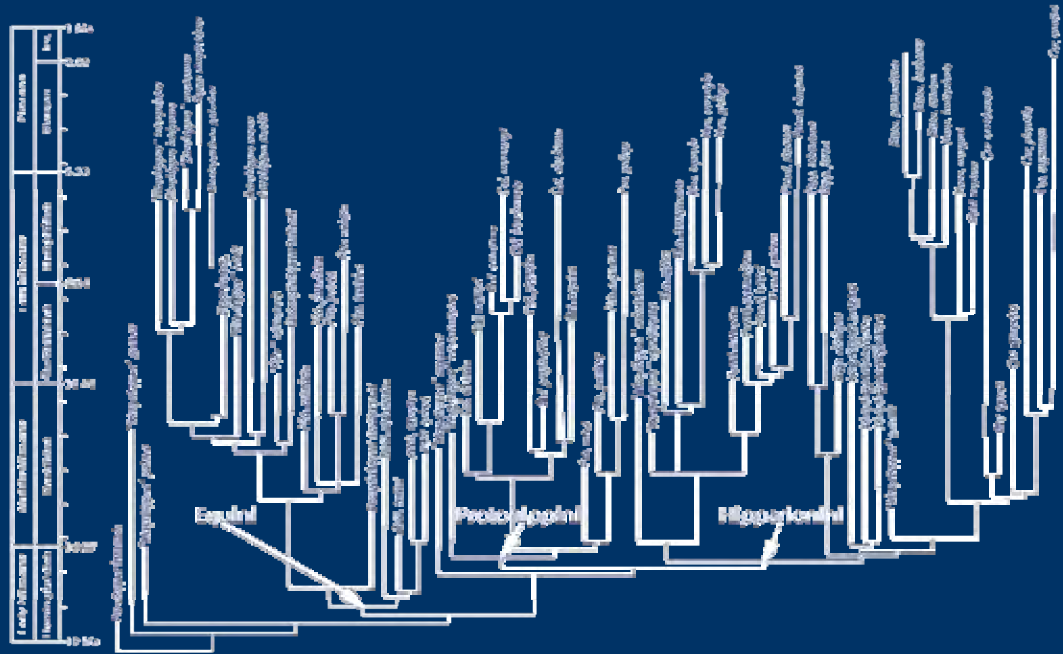
Speciation mode

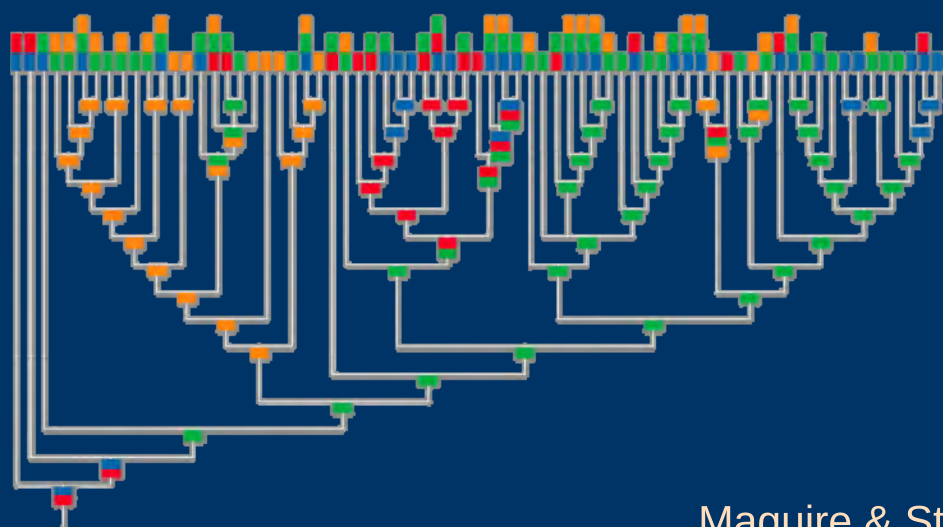


Relationship of biogeographic areas



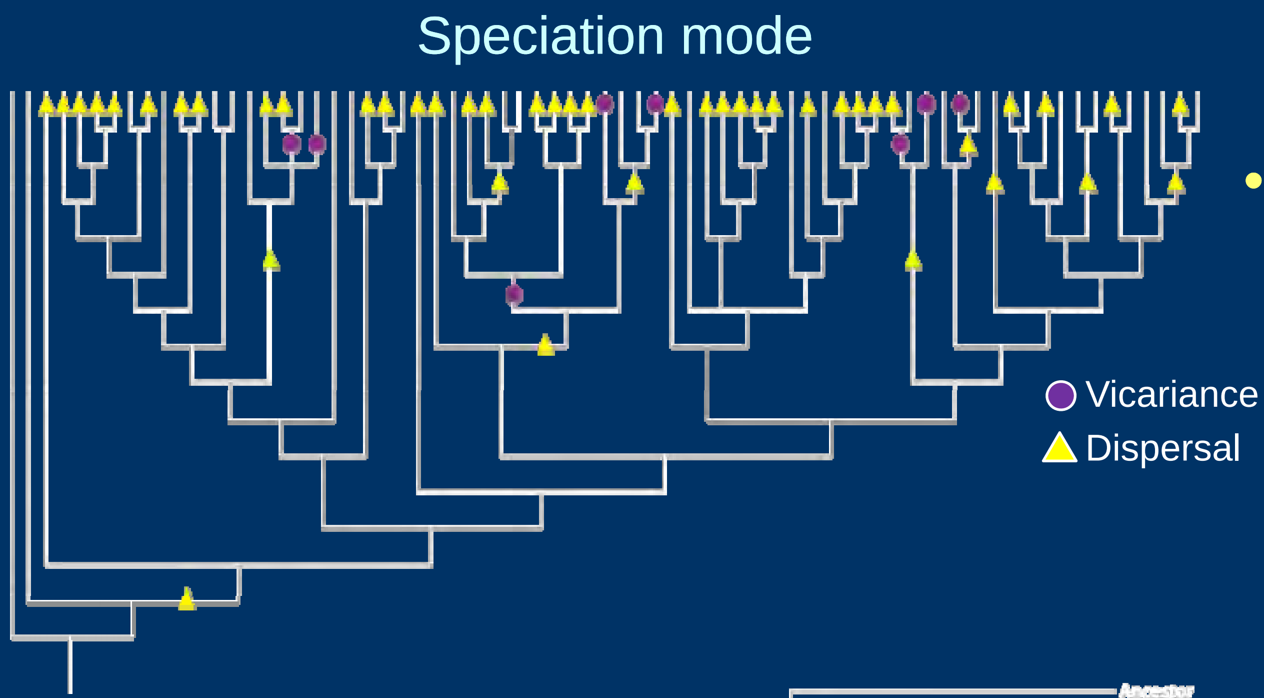
Example 1: Miocene Equinae





Maguire & Stigall (2008), Palaeo^3

Equid Phylogentic Biogeography

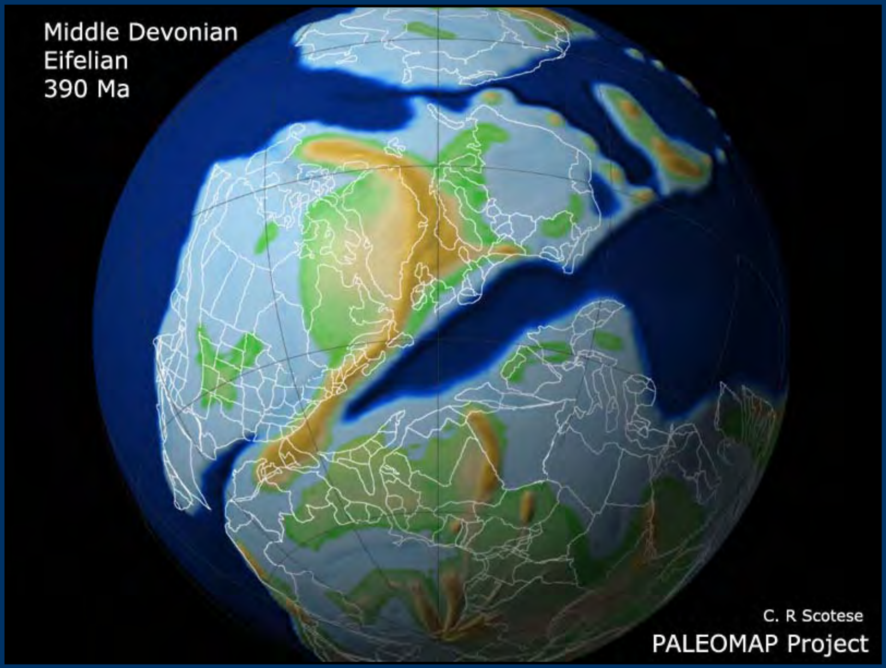


- Dispersal dominant mode of speciation

- Cyclical processes drive evolution of area relationships

Maguire & Stigall (2008), Palaeo[3]

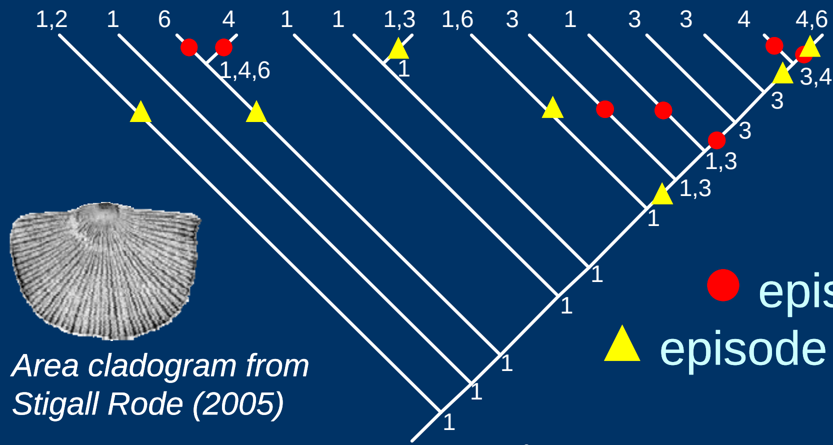
Example 2: Late Devonian Biodiversity Crisis



- Species invasions due to continental assembly and trangressions resulted in greatly reduced faunal endemism
- Extinction rates elevated
- Speciation rates depressed

	North America: Western	North America: Central	North America: Eastern	Europe N. Africa	Northern South America
Late Devonian	**Cosmopolitan Fauna**				
Middle Devonian	**Great Basin/Old World**	**Michigan**	**ENA**	**Old World**	**Old World/ Venezuelan-Columbian**

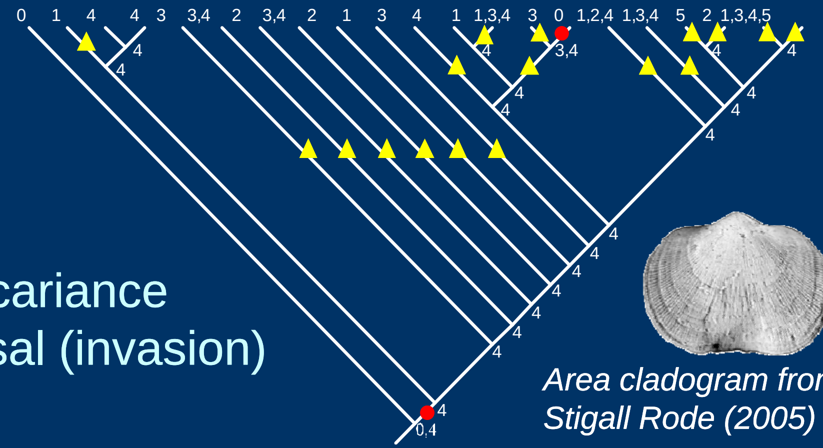
Late Devonian Speciation Mode



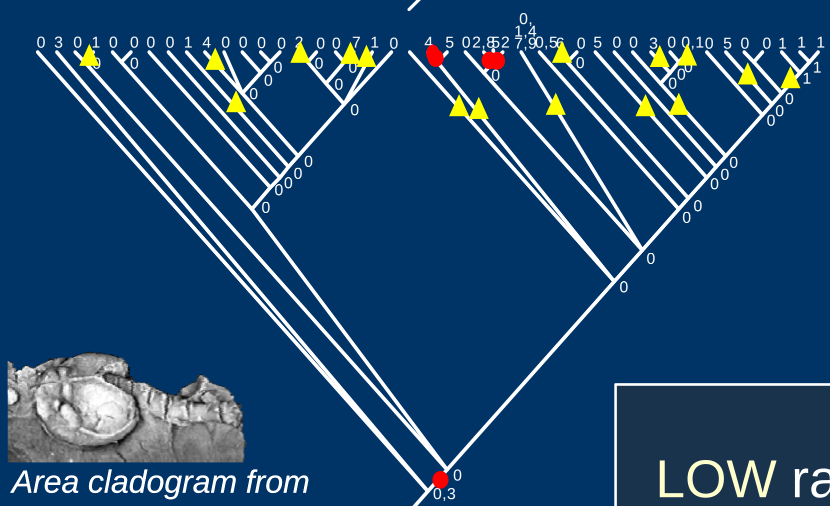
Area cladogram from Stigall Rode (2005)

● episode of vicariance

▲ episode of dispersal (invasion)

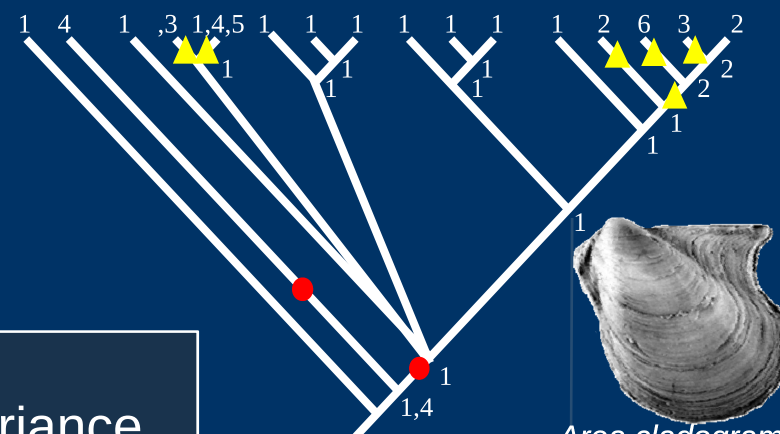


Area cladogram from Stigall Rode (2005)



Area cladogram from Rode & Lieberman (2002)

Overall,
LOW rates of vicariance,
but rampant dispersal



Area cladogram from Rode (2004)

- Low vicariance due to lack of opportunities for isolation during invasive regime & contributed to speciation rate decline

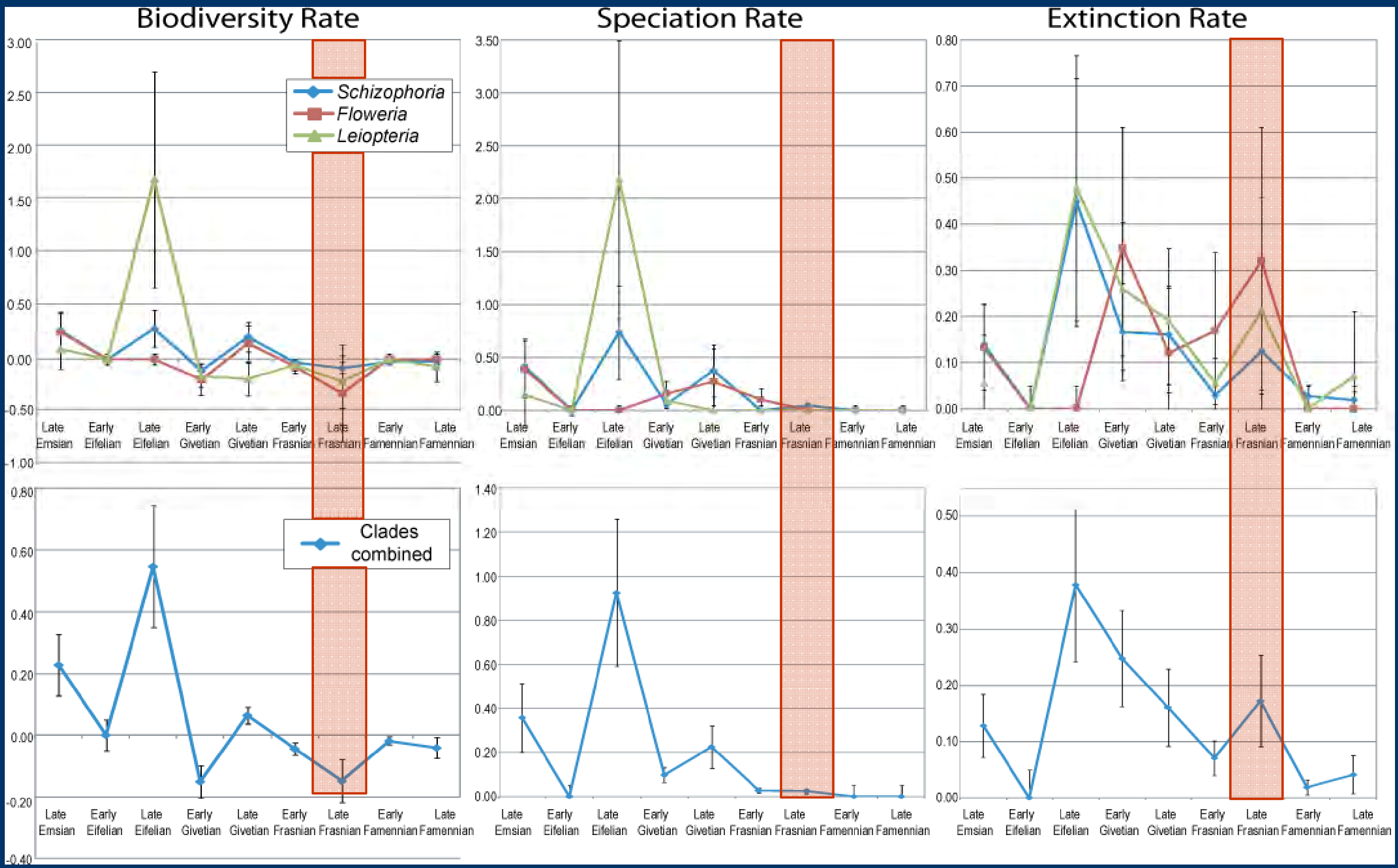
Late Devonian Speciation Mode

- Speciation by vicariance virtually non-existent
  - All speciation via dispersal (i.e. species invasions)

Clade	Number of vicariance events	Number of dispersal events	Percent speciation by vicariance	Percent speciation by dispersal
Schizophoria (Schizophoria)	2	17	11%	89%
Floweria	7	7	50%	50%
Leptodesma (Leiopteria)	2	6	25%	75%
Archaeostraca	6	13	32%	68%
Overall	17	43	28%	72%
Modern Fauna			70%	30%

Stigall & Lieberman (2006), J. Biogeography

Late Devonian Speciation Rate

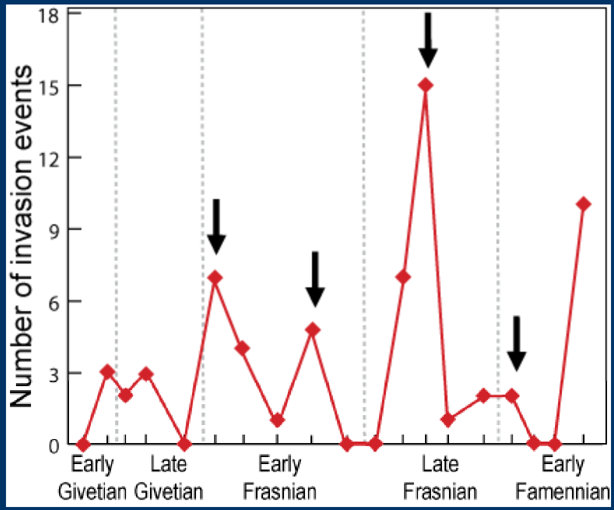


- Extinction not elevated above background during Late Devonian
- Speciation rate declines to near zero

Stigall (2008)

Late Devonian Speciation Summary

- During the Late Devonian crisis interval:
  - Speciation rates approach zero
  - Extinction elevated, but not in excess of background rates
- Numerous inter-basinal species invasions observed
- Speciation by vicariance virtually non-existent
  - All speciation via dispersal (i.e. species invasions)
- Breakdown of biogeographic and paleoecologic barriers resulted in shutdown of allopatric speciation

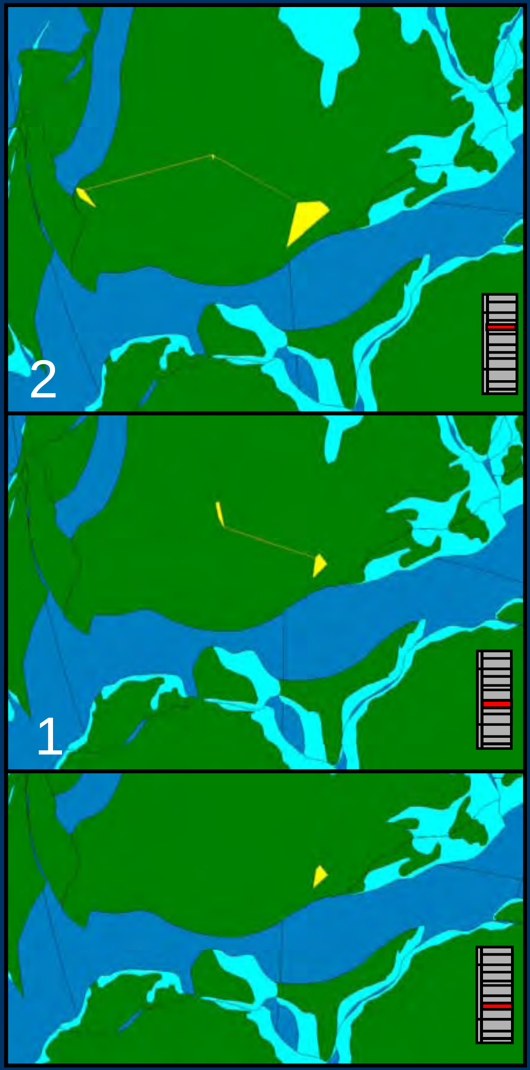


Rode & Lieberman (2004), Palaeo[3]

Integrated biogeographic approach, part II

Relationship between biogeography & paleoecology

- Research questions
  - Range contractions and expansions
  - Niche evolution vs. niche constancy
  - Habitat tracking of communities vs. individualistic species response
- Tools: GIS-based analyses incorporating environmental variables
  - Provides data amenable to statistical methods of hypothesis testing

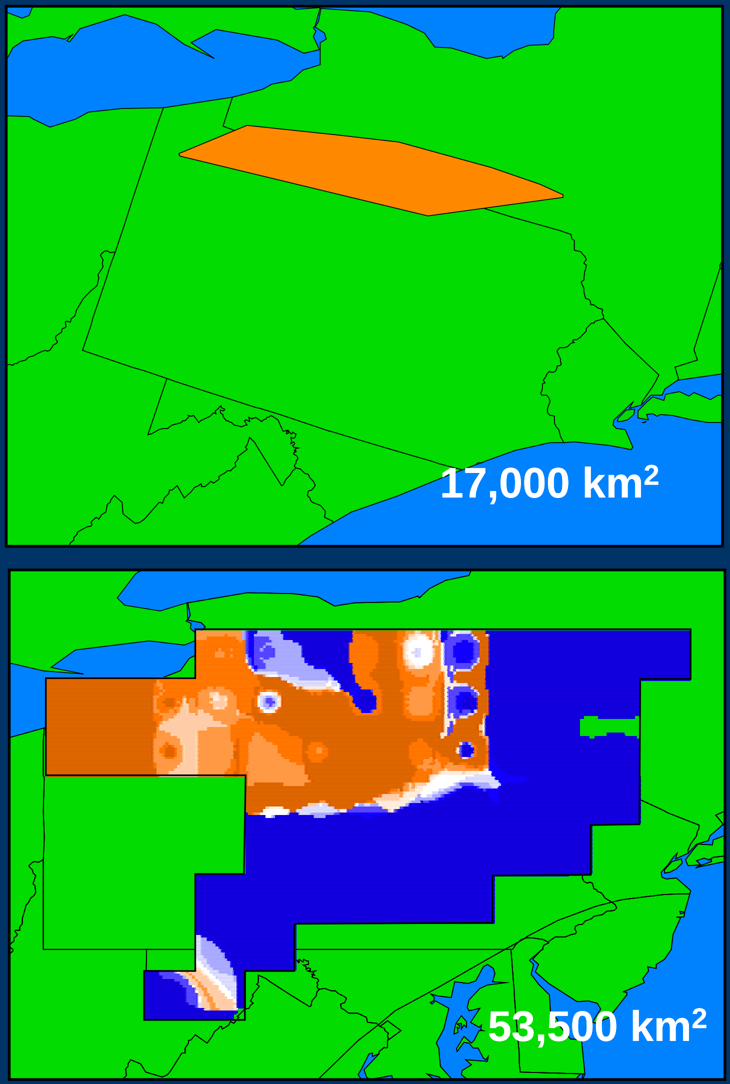


Methods of quantitative range modeling

GIS based approaches

- Polygon enclosure models
  - Requires robust set of species occurrence data
  - Create minimum convex hulls
- Ecological niche models
  - Requires (1) robust set of species occurrence data AND (2) robust set of environmental parameters determined from sedimentological proxies

Praewaagenoconcha speciosa

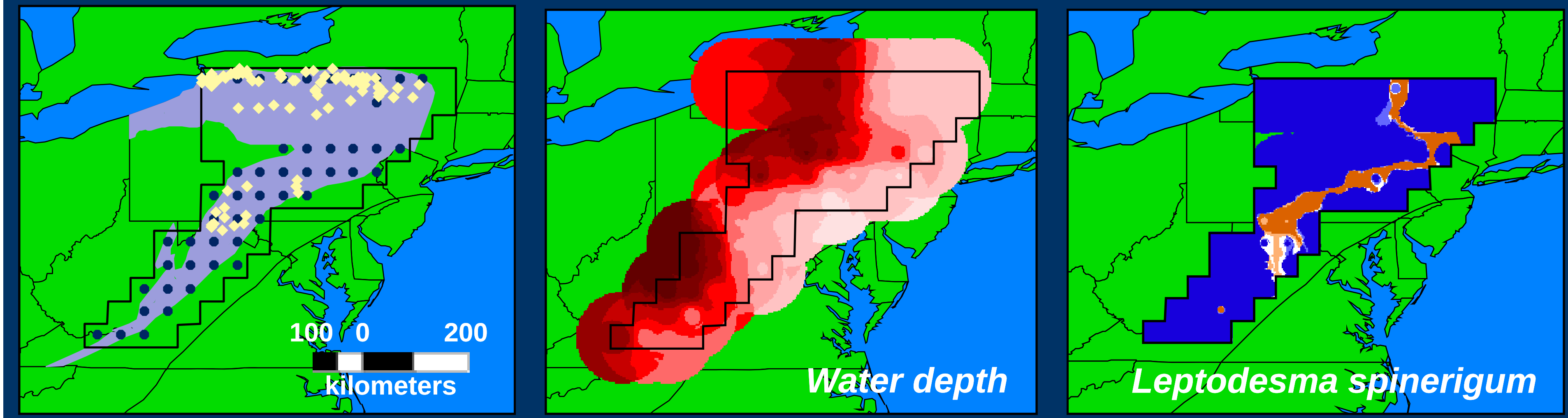


Stigall Rode & Lieberman (2005)

Environmental data and interpolation

Ecological Niche Models

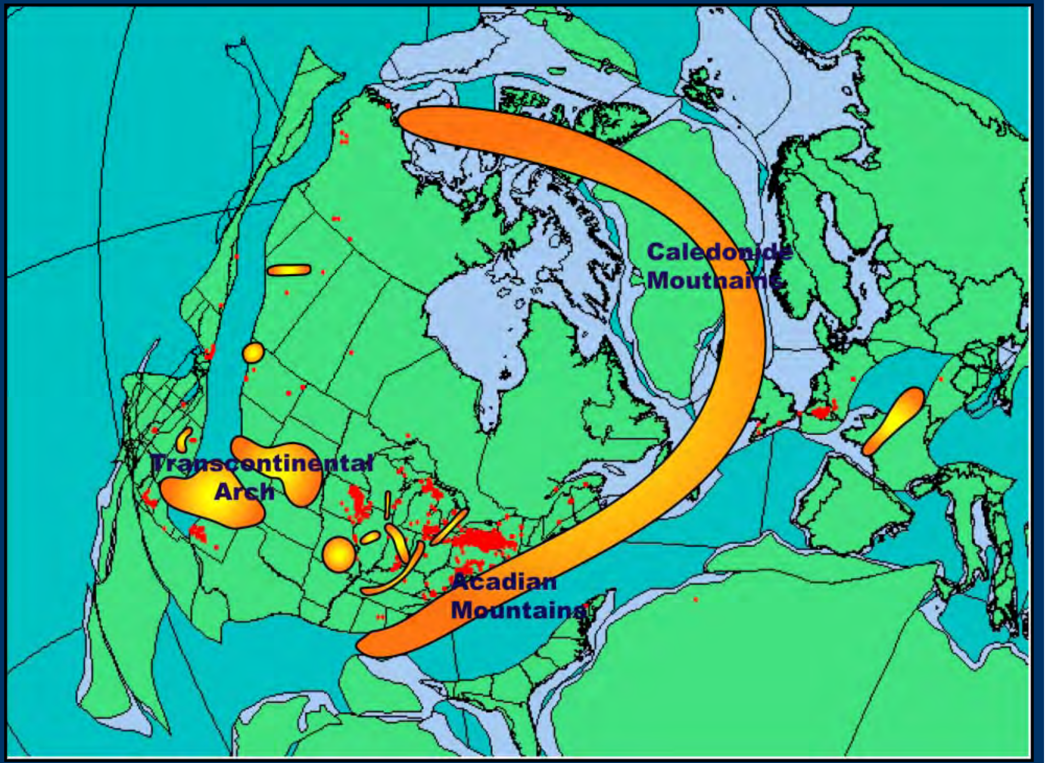
- Predict species' ranges to occupy the geographic extent of the fundamental niche
- Utilize computer learning based (genetic) algorithm to estimate species' fundamental niche from a set of known occurrence sites and environmental data



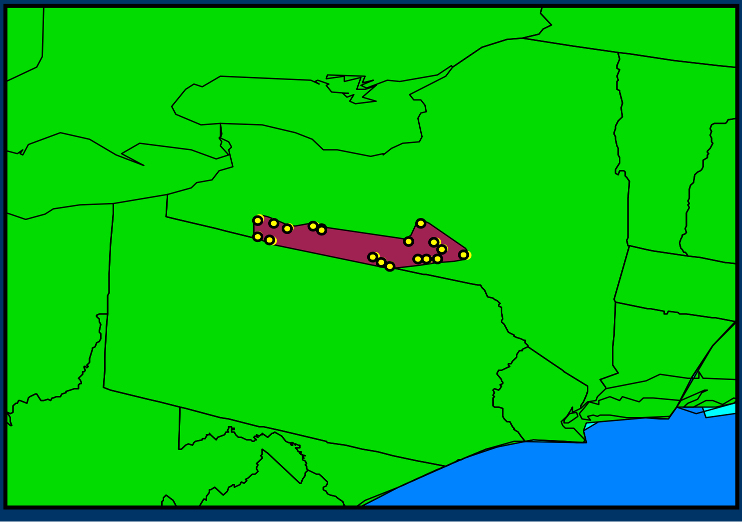
Stigall Rode & Lieberman (2005)

Example 2: Late Devonian Biodiversity Crisis

- GIS-based geographic range reconstruction (methods of Rode & Lieberman, 2000; detailed in Stigall, 2006)
- Over 5000 data points used to reconstruct ranges of 341 species in 19 temporal bins (Rode & Lieberman, 2004)



Geographic distribution of data



Range of *Tylothyris mesacostalis* during Early *rhenana* zone (Late Frasnian): 10,309 km^2

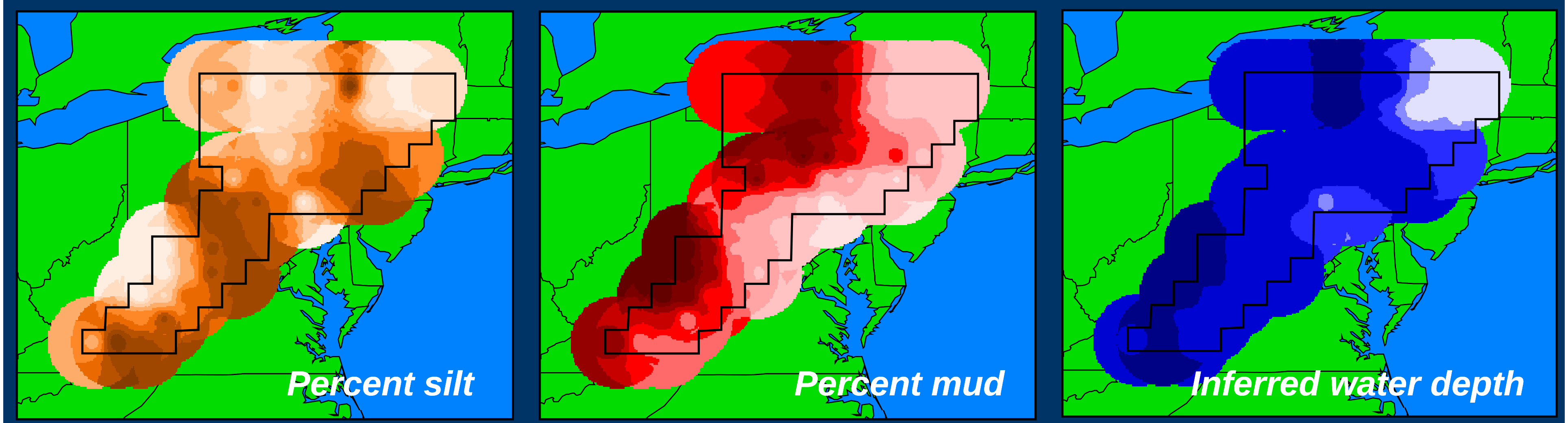
Rode & Lieberman (2004), $Palaeo^3$

Example 2: Late Devonian Biodiversity Crisis

ENM analysis

- Species occurrence data combined with nine environmental factors:

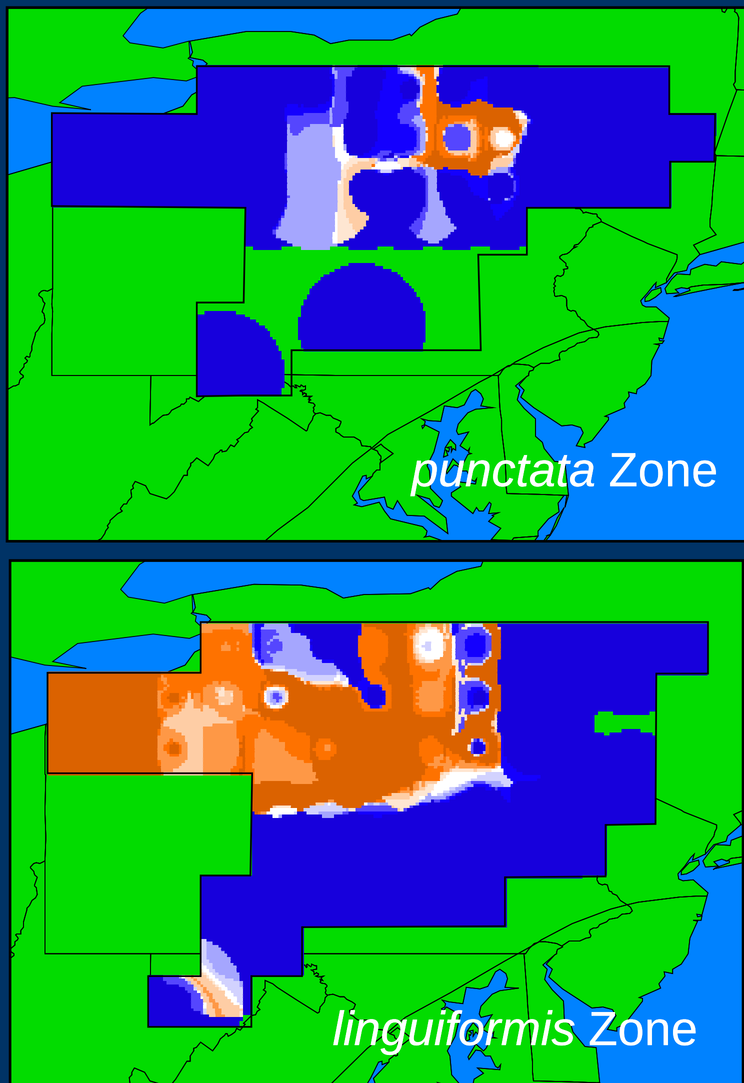
Percent mud, silt, sand	Oxygenation	Substrate type
Percent limestone	Ichnofacies	Biofacies
Depositional environment	Bedding style	Water depth



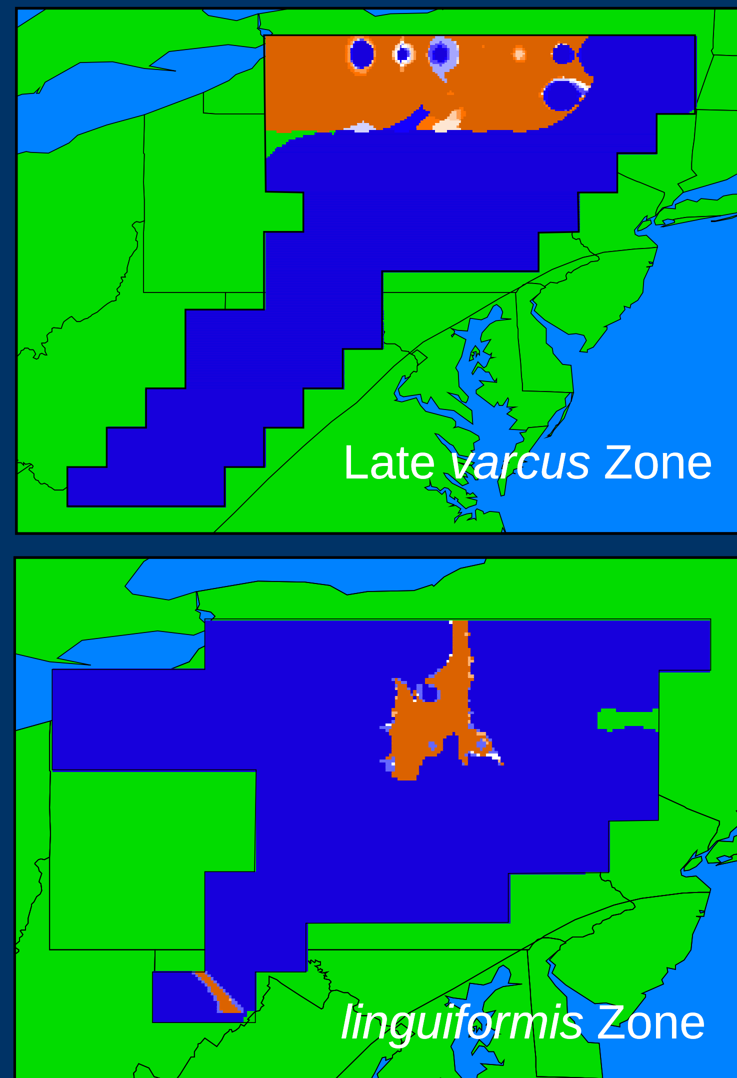
Stigall Rode & Lieberman (2005)

Temporal range change

Praewaagenoconcha speciosa



Cariniferella carinata



Stigall Rode & Lieberman (2005)

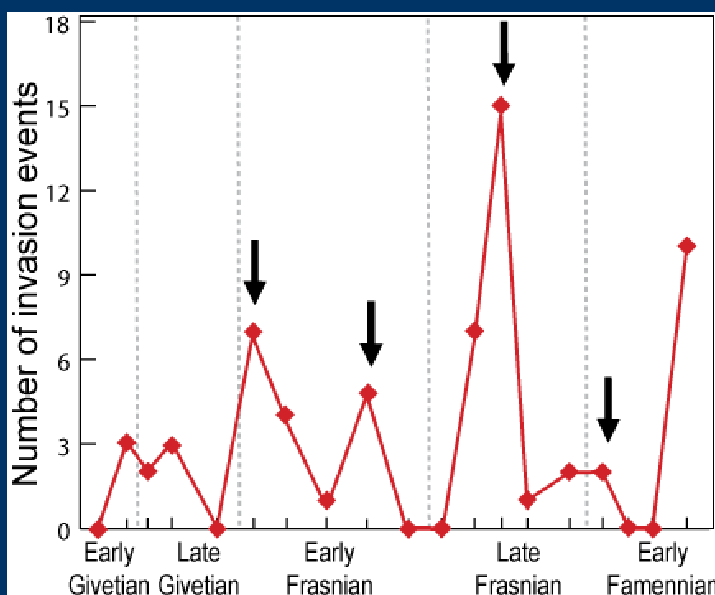
Identify interbasinal species invasions

Example: *Pseudatrypa devoniana*

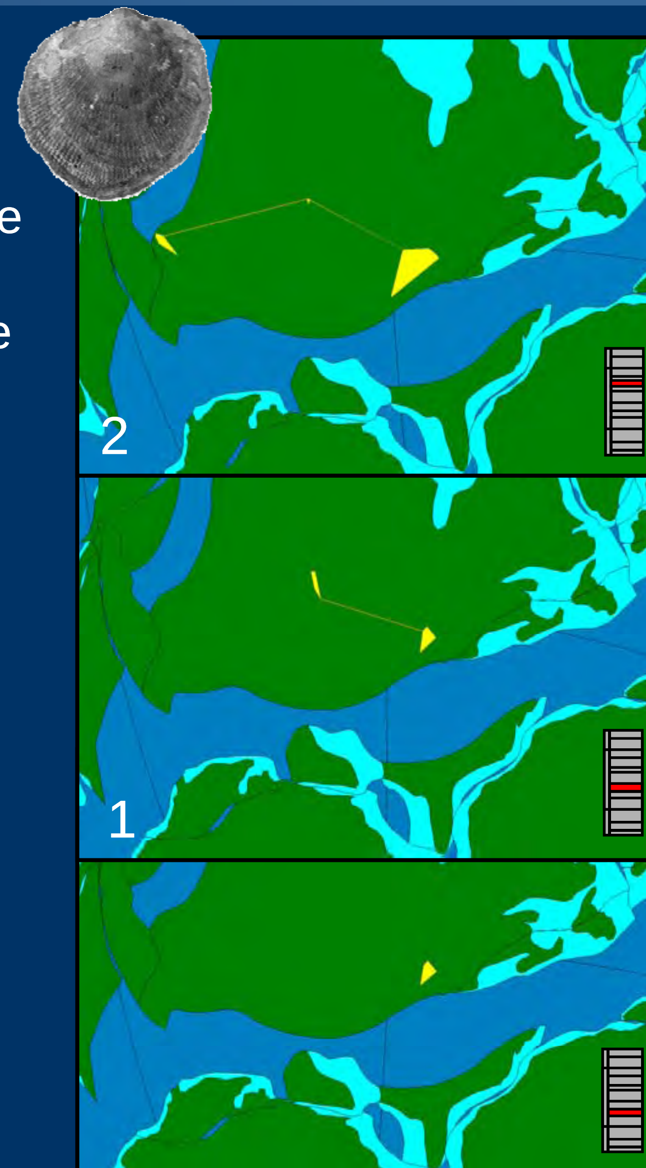
Two invasion events:

1) Appalachian to Iowa basins in *punctata* zone (mid Frasnian, onset of TR cycle IIc)
2) Iowa to New Mexico basins in *rhenana* zone (Late Frasnian, onset of TR cycle IId)

Total interbasinal invasions



Stigall & Lieberman (2006), J Biogeo



Rode & Lieberman (2004), Palaeo[3]

Examine survival vs. geographic range

1. Comparison of geographic range size vs. survival

Victims	Survivors
N=30	N=127
Mean range: 6212	Mean range: 15446
SE mean: 895	SE mean: 3592

T-test: H_o: $\mu_s > \mu_v$ N=157 p= 0.009

2. Comparison of survival status vs. invasive history

X^2 table

	Invasive species	Non-invasive species
Extinct	**18** **27.86**	**109** **99.14**
Survive	**16** **6.14**	**12** **21.86**

N= 155 p<< 0.001

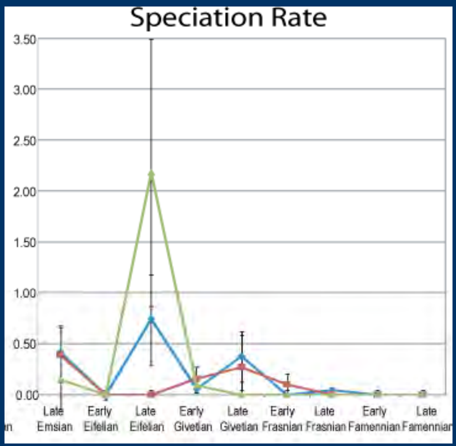
observed/ expected O>E

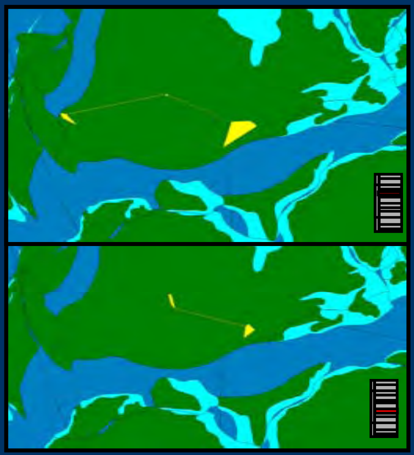
Rode & Lieberman (2004), Palaeo[3]

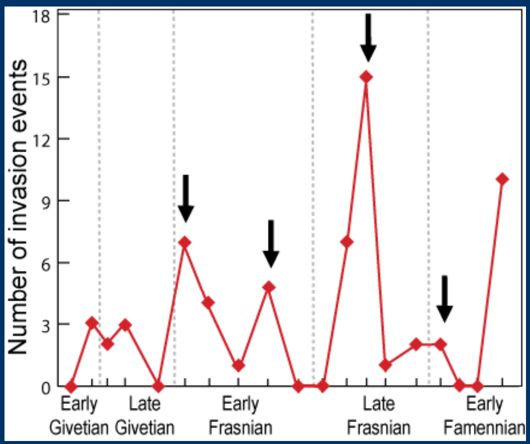
Integrated biogeographic approach III

Complex feedback loops between biogeography, paleoecology, and macroevolution

- Research questions:
  - Biodiversity crises
  - Interbasinal invasion / biotic interchange events
- Tools: integrated analyses of phylogenetic and environmental patterns

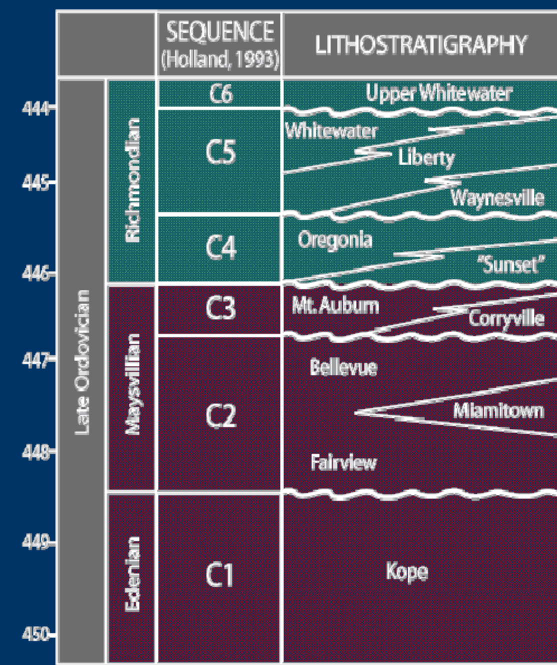






Case Study 3: Richmondian Invasion

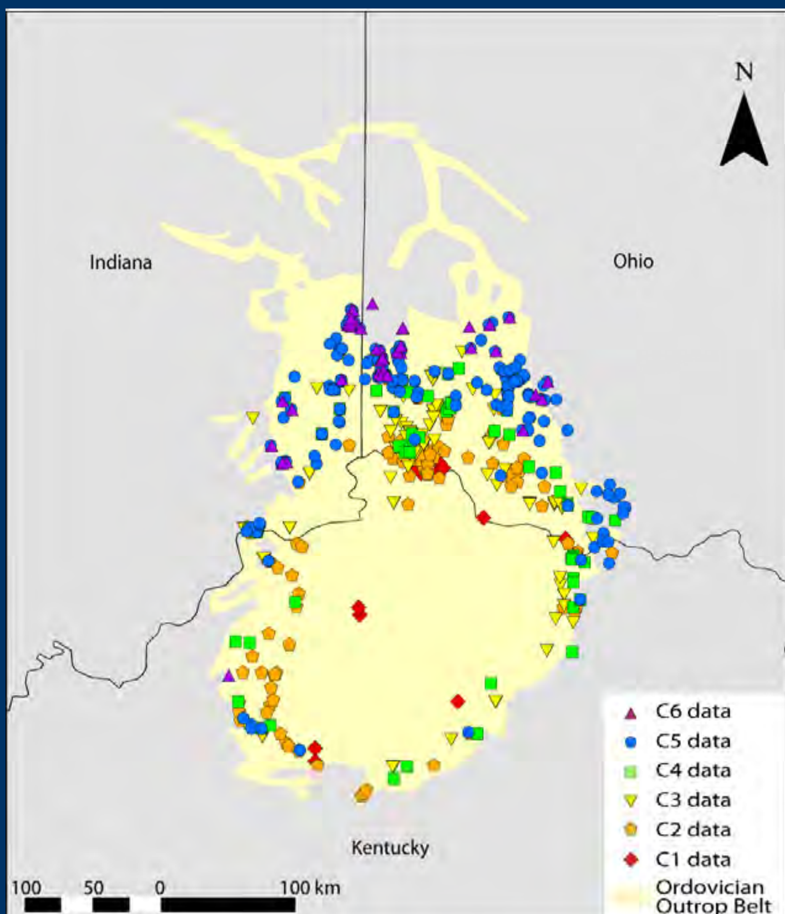
- Late Ordovician invasion of taxa from W. North America into ENA
- Related to oceanographic changes
(Holland & Patzkowsky, 1997)
- Ecological patterns well characterized
(Holland & Patzkowsky, 2007)



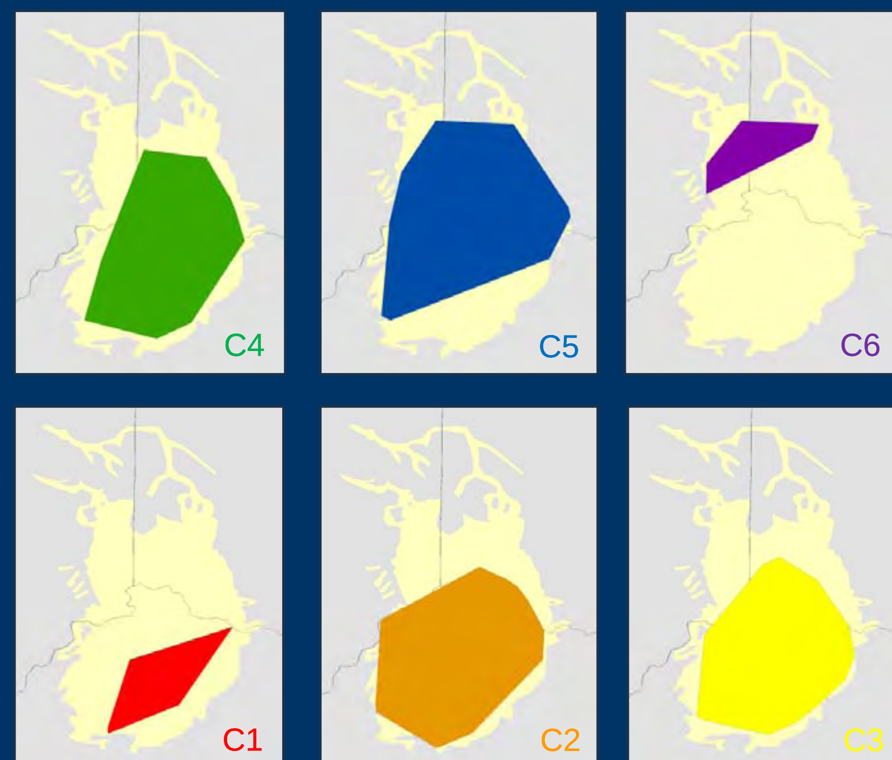
Stratigraphic framework
(after Holland & Patzkowsky, 1996)

GIS-based geographic range reconstruction

Entire species occurrence data set



Geographic range of *Hebertella occidentalis*



Stigall & Smith, in review

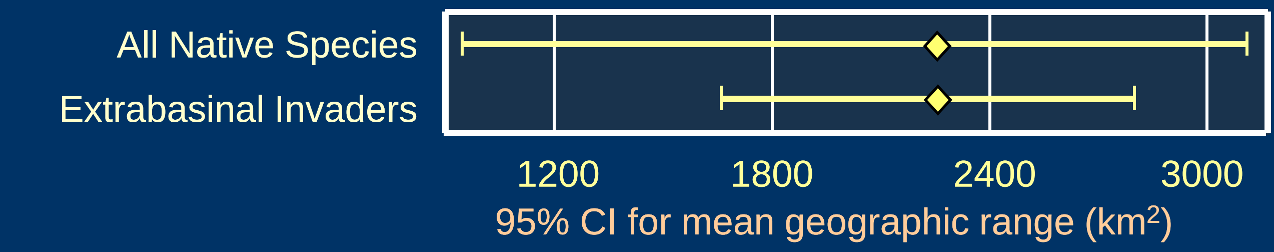
Stratigraphic distribution of species

	Species	C1	C2	C3	C4	C5	C6
Native species: Restricted to Maysvillian	*Dalmanella multisecta*	-------	-------				
	Leptaena gibbosa	-------					
	Platystrophia auburnensis			-------			
	Platystrophia corryvillensis			-------			
	Platystrophia crassa		-------	-------			
	Platystrophia hopensis	-------	-------	-------			
	Platystrophia morrowensis			-------			
	Platystrophia sublaticosta		-------	-------			
	Plectorthis aequivalis		-------	-------			
	Plectorthis fissicosta		-------				
	Plectorthis neglecta		-------				
	Plectorthis plicatella		-------				
	Sowerbyella rugosa	-------					
	Strophomena maysvillensis	-------	-------				
	Strophomena planoconvexa	-------	-------				
	Zygospira cincinnatiensis	-------	-------				
Native species: Carryover to Richmondian	*Dalmanella meeki*			-------	-------	-------	-------
	Hebertella occidentalis	-------	-------	-------	-------	-------	-------
	Hebertella subjugata		-------			-------	-------
	Platystrophia cypha		-------	-------	-------	-------	-------
	Platystrophia laticosta		-------	-------	-------	-------	
	Platystrophia ponderosa	-------	-------	-------	-------		
	Rafinesquina alternata	-------	-------	-------	-------	-------	-------
	Zygospira modesta	-------	-------	-------	-------	-------	-------
Descendants of native species: Speciate in Richmondian	*Hebertella alveata*					-------	-------
	Platystrophia acutilirata					-------	-------
	Platystrophia annieana					-------	
	Platystrophia clarksvillensis				-------	-------	-------
	Platystrophia cummingsi					-------	
	Platystrophia elkhornensis					-------	-------
	Platystrophia forestei					-------	
	Platystrophia moritura					-------	-------
	Strophomena concordensis				-------	-------	
	Strophomena nutans					-------	
	Strophomena planumbona				-------	-------	-------
	Strophomena sulcata					-------	-------
	Strophomena vetusta					-------	-------
Richmondian extrabasinal invaders	*Austinella scovellei*					-------	
	Catazyga schuchertana					-------	
	Eochonetes clarksvillensis					-------	-------
	Glyptorthis insculpta					-------	-------
	Hiscobeccus capax					-------	-------
	Holtedahlina sulcata					-------	-------
	Lepidocyclus perlamellosum					-------	
	Leptaena richmondensis				-------	-------	-------
	Plaesiomys subquadrata					-------	-------
	Retrorsirostra carleyi				-------	-------	
	Rhynchotrema denatum				-------	-------	-------
	Tetraphalerella neglecta					-------	

Stigall & Smith, in review

Native species vs. extrabasinal invaders

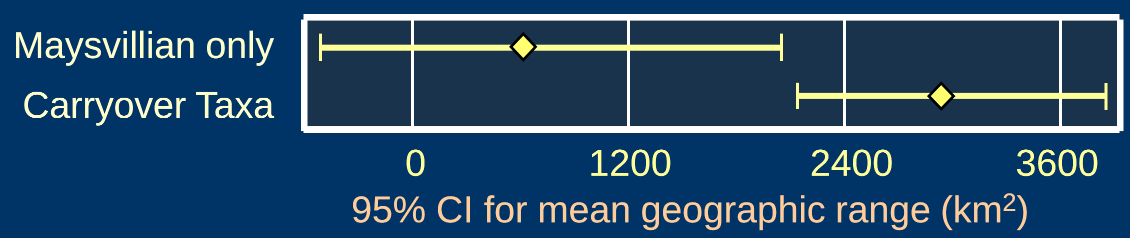
1. Comparison of geographic range of native vs. invasive species



T-test: N = 59

p = 0.998

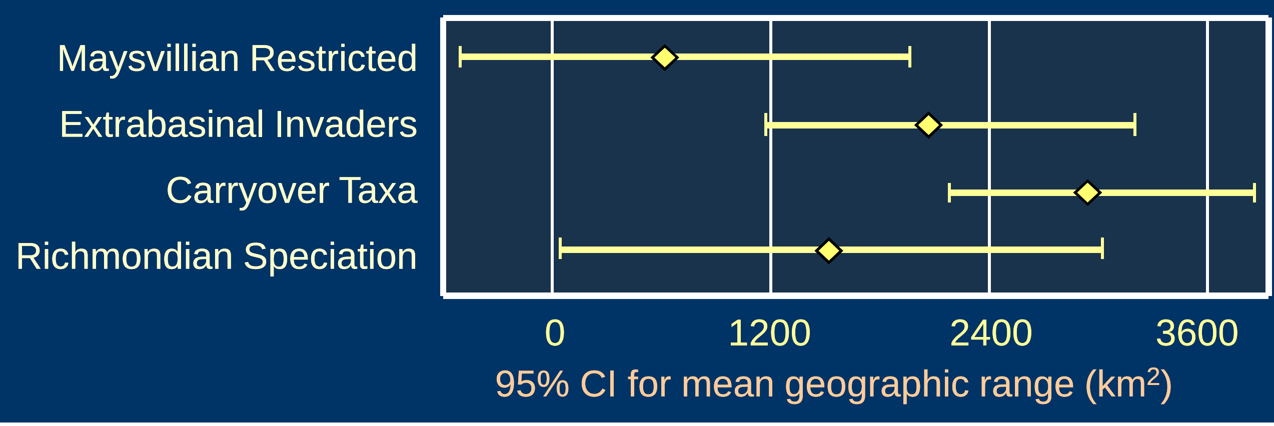
2. Comparison of survival status of native species vs. geographic range



T-test: N = 39

$p < 0.0005$

3. Comparison of species groups vs. geographic range

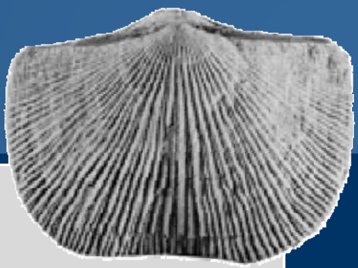


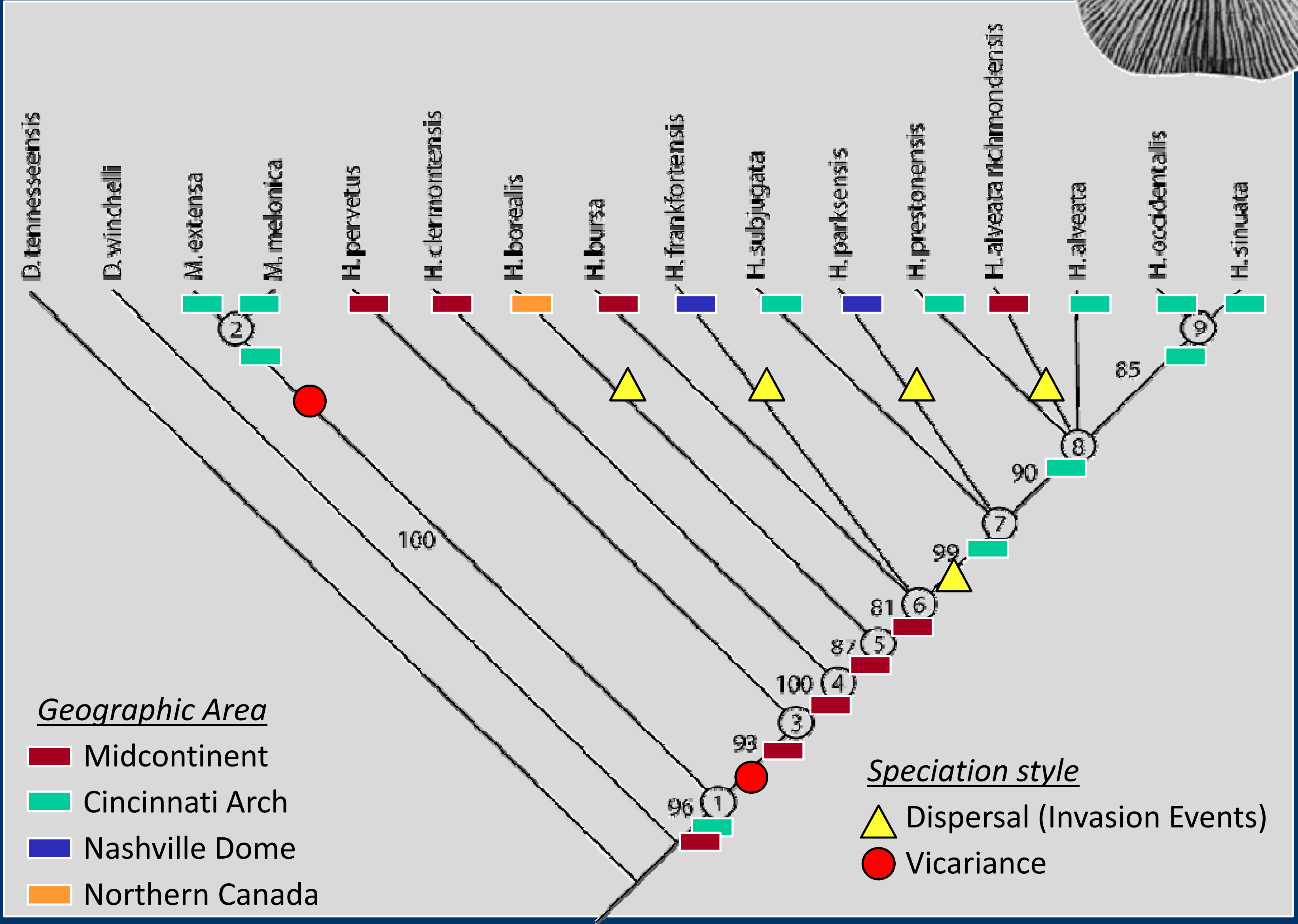
ANOVA: N = 59

p = 0.025

Stigall, 2008

Hebertella phylogeny & biogeography





Klingensmith (2007)

Integrating historical and ecological paleobiogeography

- Provides clues to evolutionary patterns and feedbacks often masked in single approach analyses

- In the Late Devonian and Late Ordovician case studies:
  - Preferential survival of species with wide geographic ranges (=ecological generalists)
  - Preferential survival of invader taxa (typically ecological generalists)
  - Reduced opportunities for vicariance
  - Decline in overall speciation rate
  - Increased invasions result in decreased speciation

Conclusions

- Quantitative methods provide new analytical rigor to paleobiogeography
- Potential to analyze complex paleobiological patterns
- Capacity for hypothesis testing and generation

Emerging research questions

- Relationship between species ranges and speciation
- Range expansion and contraction under shifting paleoecological regimes
- Impact of invasive species on community structure and macroevolutionary dynamics
- Mechanics of transitions between endemic and cosmopolitan faunas
- How ecology and geographic range impact extinction during both background and crisis intervals

Acknowledgements

- Collaborators: Bruce Lieberman
- Students: B. Klingensmith, K. Maguire, J. Smith
- Funding: Ohio University, ACS's Petroleum Research Fund

Referenced papers & figure sources

- Klingensmith, B.C., 2007. GIS-based biogeography of Cincinnatian (Upper Ordovician) brachiopods with special reference to *Hebertella.* Unpublished MS thesis, Ohio University, Athens, Ohio.
- Maguire, K.C., and Stigall, A.L. 2008. Paleobiogeography of Miocene Equinae of North America: A phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal. Palaeogeography, Palaeoclimatology, Palaeoecology, 267: 175-184.
- Rode, A.L., and Lieberman, B.S. 2002. Phylogenetic and biogeographic analysis of Devonian phyllocarid crustaceans. Journal of Paleontology, 76(2): 269-284.
- Rode, A.L., and Lieberman, B.S. 2004. Using GIS to unlock the interactions between biogeography, environment, and evolution in Middle and Late Devonian brachiopods and bivalves. Palaeogeography, Palaeoclimatology, Palaeogeography, 211(3-4): 345-359.
- Rode, A.L. 2004. Phylogenetic revision of the Devonian bivalve, *Leptodesma (Leiopteria)*. Yale University Postilla, 229: 1-26.
- Rode, A.L., and Lieberman, B.S. 2005. Integrating biogeography and evolution using phylogenetics and PaleoGIS: A case study involving Devonian crustaceans. Journal of Paleontology, 79(2): 267-276.
- Stigall, A.L. 2008. Tracking species in space and time: Assessing the relationships between paleobiogeography, paleoecology, and macroevolution, p. 227-242. *In* P. H. Kelly and R. K. Bambach (eds.) From Evolution to Geobiology: Research Questions Driving Paleontology at the Start of a New Century. The Paleontological Society Papers, volume 14.
- Stigall, A.L. 2008. Integrating GIS and phylogenetic biogeography to assess species-level biogeographic patterns: A case study of Late Devonian faunal dynamics. *In* P. Upchurch, A. McGowan, and C. Slater, (eds.), Palaeogeography and Palaeobiogeography: Biodiversity in Space and Time. CRC Press, expected publication December, 2008.
- Stigall, A.L., and Lieberman, B.S. 2006. Quantitative Paleobiogeography: GIS, Phylogenetic Biogeographic Analysis, and Conservation Insights. Journal of Biogeography, 33 (12): 2051-2060.
- Stigall, A.L., and J. Smith. GIS-based analysis of brachiopod biogeography in the type Cincinnatian: Quantifying biogeographic shifts across an the Richmondian Invasion. Palaeontologica Electronica, in prep.
- Stigall Rode, A.L. 2005. Systematic revision of the Devonian brachiopods *Schizophoria (Schizophoria)* and "*Schuchertella*" from North America. Journal of Systematic Palaeontology, 3(2): 133-167.
- Stigall Rode, A.L., and Lieberman, B.S. 2005. Using environmental niche modelling to study the Late Devonian biodiversity crisis, p. 93-180. *In* D. J. Over, J. R. Morrow, and P .B. Wignall (eds.), Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach. Developments in Palaeontology and Stratigraphy, Elsevier, Amsterdam.
- Stigall Rode, A.L., and Lieberman, B.S. 2005. Paleobiogeographic patterns in the Middle and Late Devonian emphasizing Laurentia. Palaeogeography, Palaeoclimatology, Palaeoecology, 222 (3-4): 272-284.