Extinction and Speciation in the North American Flora in Response to Quaternary Climate Changes

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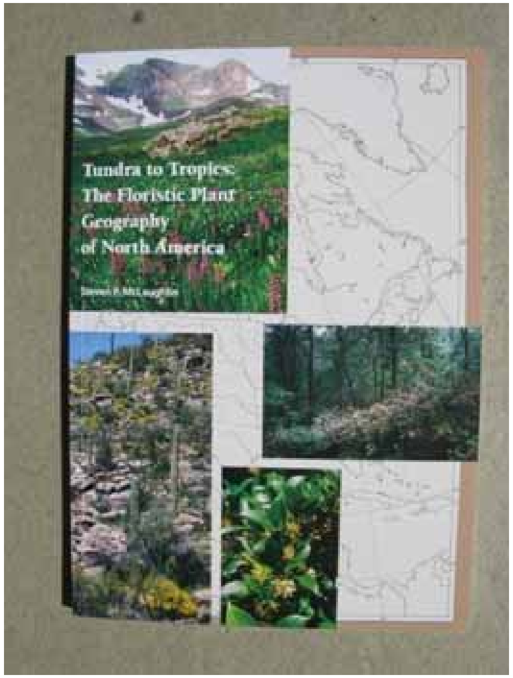
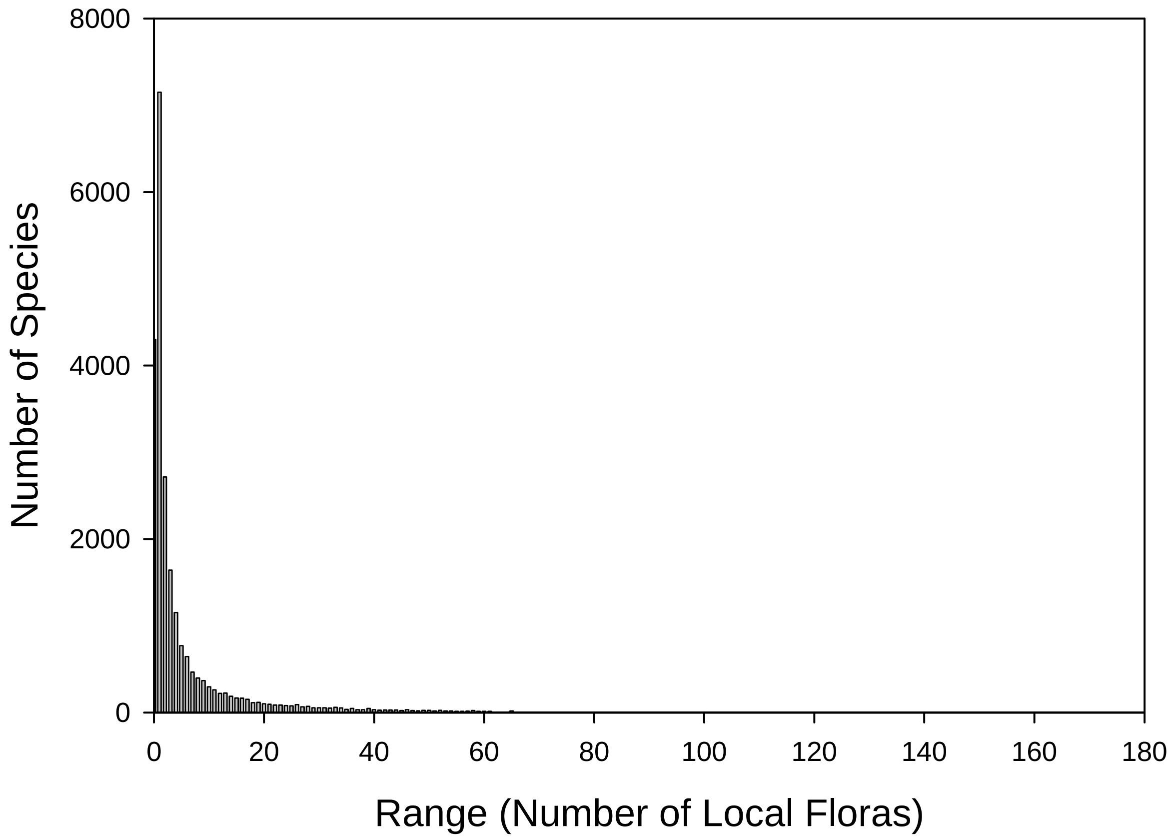
Climate, Ecosystems and Resources in Eastern California

November 7, 2008

Frequency distribution for 19,000 species of vascular plants recorded in 245 local floras from Canada, USA and Mexico (McLaughlin, 2007)





This left-skewed frequency distribution has been called "… one of the most fundamental and interesting areographic patterns …." (Lomolino et al., 2006, *Biogeography*, 3rd Ed.)

But …

Paleontologists tell us that the fossil record shows that speciation and extinction rates are very low (0.1 to 2 speciations or extinctions per species per million years) and that migration rates are high (up to 1 km per year).

Shouldn’t low speciation and extinction rates combine with high migration rates to produce highly *right-skewed* frequency distributions, with few rare and many widespread species?

How do highly unimodal, left-skewed frequency distributions come about?

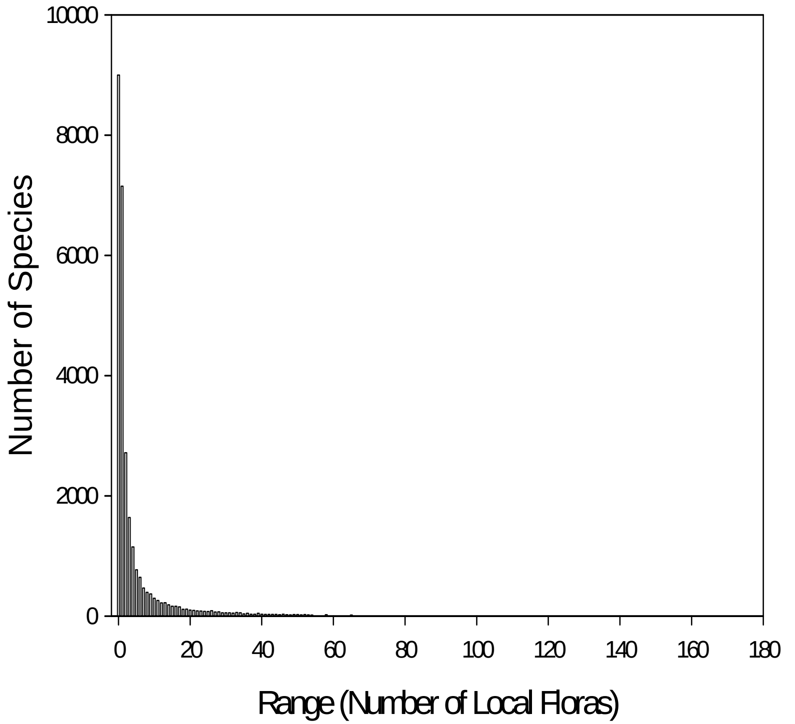
Specifically, what rates of speciation, extinction, and migration combine to produce such frequency distributions?

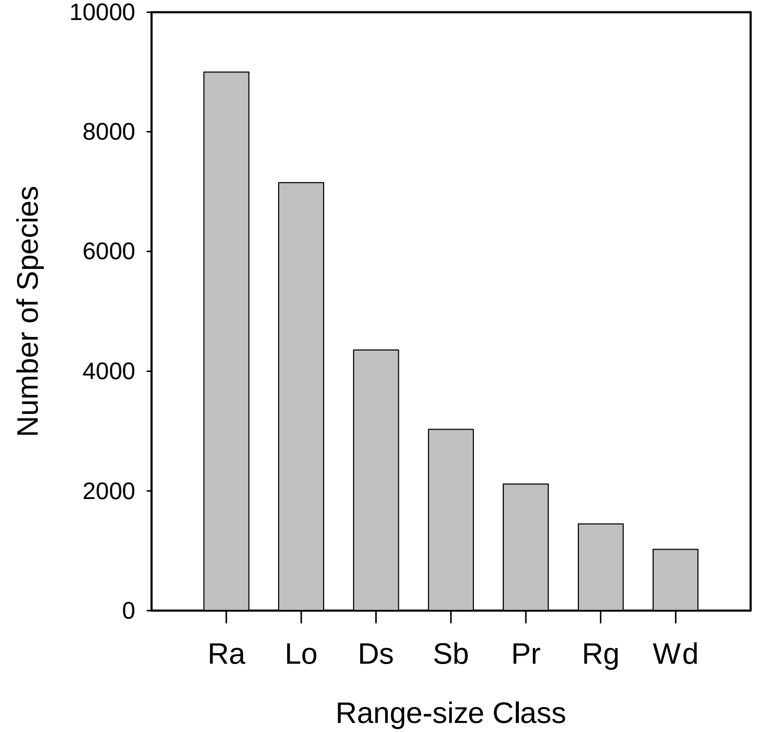
Approach: Develop a transition-probabililty matrix to model frequency distributions for 20 glacial-interglacial cycles of the Quaternary.

Need to simplify frequency distribution to a smaller number of range-size classes.

- Rare [Ra]: Not recorded from any local flora. (4300 species from the *Flora North America* area; I estimate ca. 9000 species for *FNA* area + Mexico.)
- Local [Lo]: Recorded from 1 local flora.
- District [Ds]: Recorded from 2-3 local floras.
- Subprovincial [Sb]: Recorded from 4-7 local floras.
- Provincial [Pr]: Recorded from 8-15 local floras.
- Regional [Rg]: Recorded from 16-31 local floras.
- Widespread [Wd]: Recorded from 32 or more local floras.

Log_2 Transformation of Frequency Distribution





Need to define three additional classes of species:

- An immigrant pool [IP], estimated at 10,000 species for the base-case simulations.
- Extinct species [E]
- Incipient species [IS]

“Migration” is actually several processes, each with its own probability

- Emigration from North America (into the Neotropics during glacial intervals).
- Immigration into North America (from the Neotropics during interglacial intervals).
- Range expansion
- Range contraction
- Range shifts

The model is comprised of three transition-probability matrices:

- Glacial-interval transitions [**TP(G)**]
- Interglacial-interval transitions [**TP(IG)**]
- Establishment/expansion of incipient species [**RE(IS)**]

Transition-probability Matrix 1. Glacial Intervals

	IP	E	IS	Ra	Lo	Ds	Sb	Pr	Rg	Wd
IP	1.00	0	0	*M*	*M*	*M*	0	0	0	0
E	0	1.00	0	*E*	*E*	*E*	*E*	*E*	*E*	*E*
IS	0	0	0	*IS*	*IS*	*IS*	*IS*	IS	IS	IS
Ra	0	0	0	*RS*	*RC*	*RC*	0	0	0	0
Lo	0	0	0	*RE*	*RS*	*RC*	*RC*	0	0	0
Ds	0	0	0	*RE*	*RE*	*RS*	*RC*	*RC*	0	0
Sb	0	0	0	0	*RE*	*RE*	*RS*	*RC*	*RC*	0
Pr	0	0	0	0	0	*RE*	*RE*	*RS*	*RC*	*RC*
Rg	0	0	0	0	0	0	*RE*	*RE*	*RS*	*RC*
Wd	0	0	0	0	0	0	0	*RE*	*RE*	*RS*

"Running the Model"

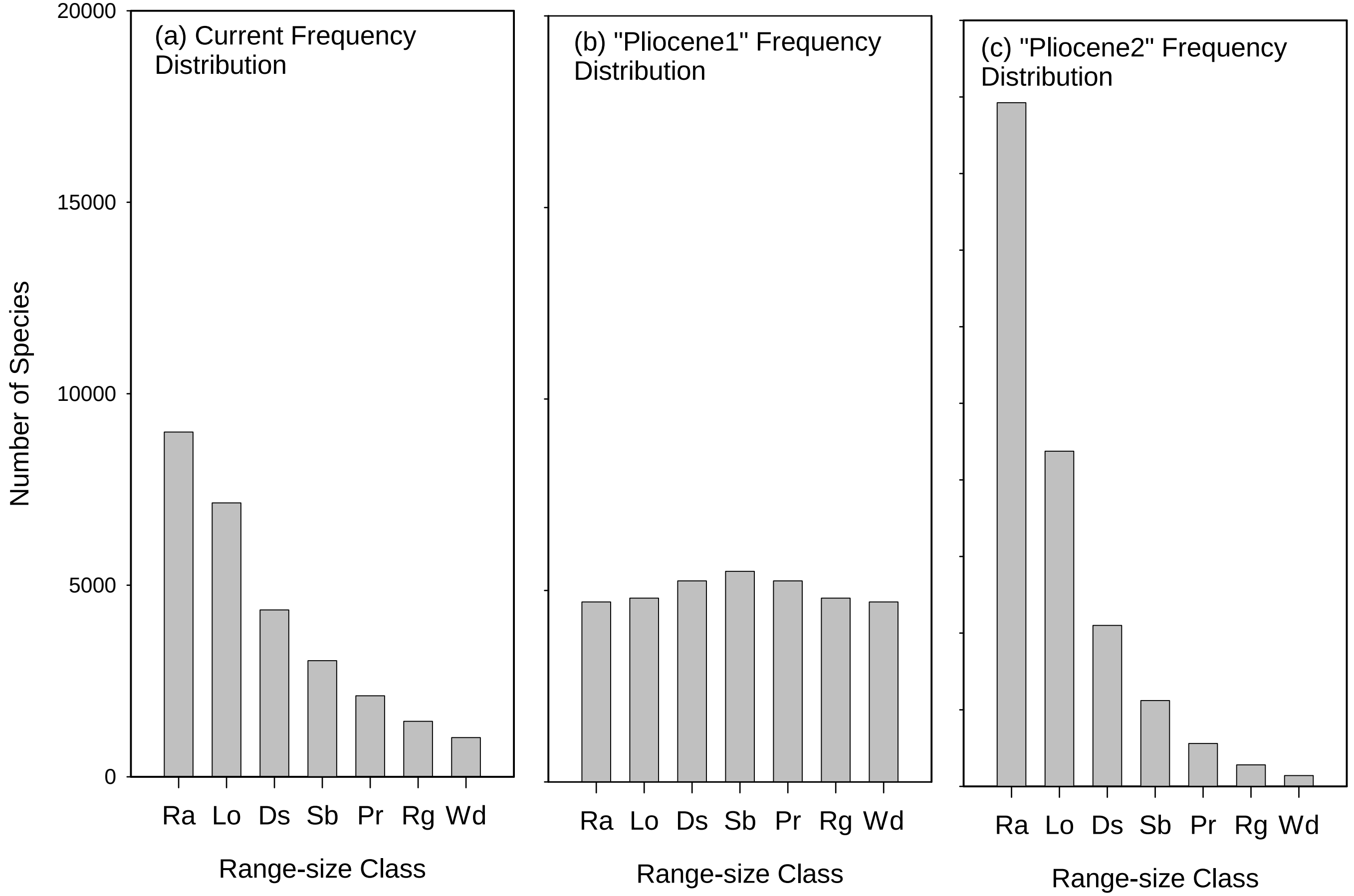
$$[\mathbf{TP}(\mathrm{G})] \times [\mathbf{FD*}_t] = [\mathbf{FD}_{t+1}]$$
$$[\mathbf{RE}(\mathrm{IS})] \times [\mathbf{FD}_{t+1}] = [\mathbf{FD*}_{t+1}]$$
$$[\mathbf{TP}(\mathrm{IG})] \times [\mathbf{FD*}_{t+1}] = [\mathbf{FD}_{t+2}]$$
$$[\mathbf{RE}(\mathrm{IS})] \times [\mathbf{FD}_{t+2}] = [\mathbf{FD*}_{t+2}]$$

Repeat 20 times.

But …

What is the initial distribution $\mathbf{FD}_{t=0}$ -- the end-Pliocene frequency distribution?

Three initial end-Pliocene distributions used to initialize simulations



Parameterizing the model: Extinction rates from the fossil record

(E = extinctions per species per million years)

Group	E	Source
Herbs	0.100	Levin & Wilson (1976)
Shrubs	0.040	Levin & Wilson (1976)
Hardwoods	0.030	Levin & Wilson (1976)
Conifers	0.020	Levin & Wilson (1976)
Woody species	0.045	Stebbins (1982)
Dicots	0.330	Nicklas et al. (1983)
Monocots	0.300	Nicklas et al. (1983)
Plants	>0.050	Standley (1985)
Conifers	0.200	Valentine et al. (1991)
Monocots	0.160	Valentine et al. (1991)
Dicots	0.260	Valentine et al. (1991)

Parameterizing the Model: Speciation rates from the fossil record

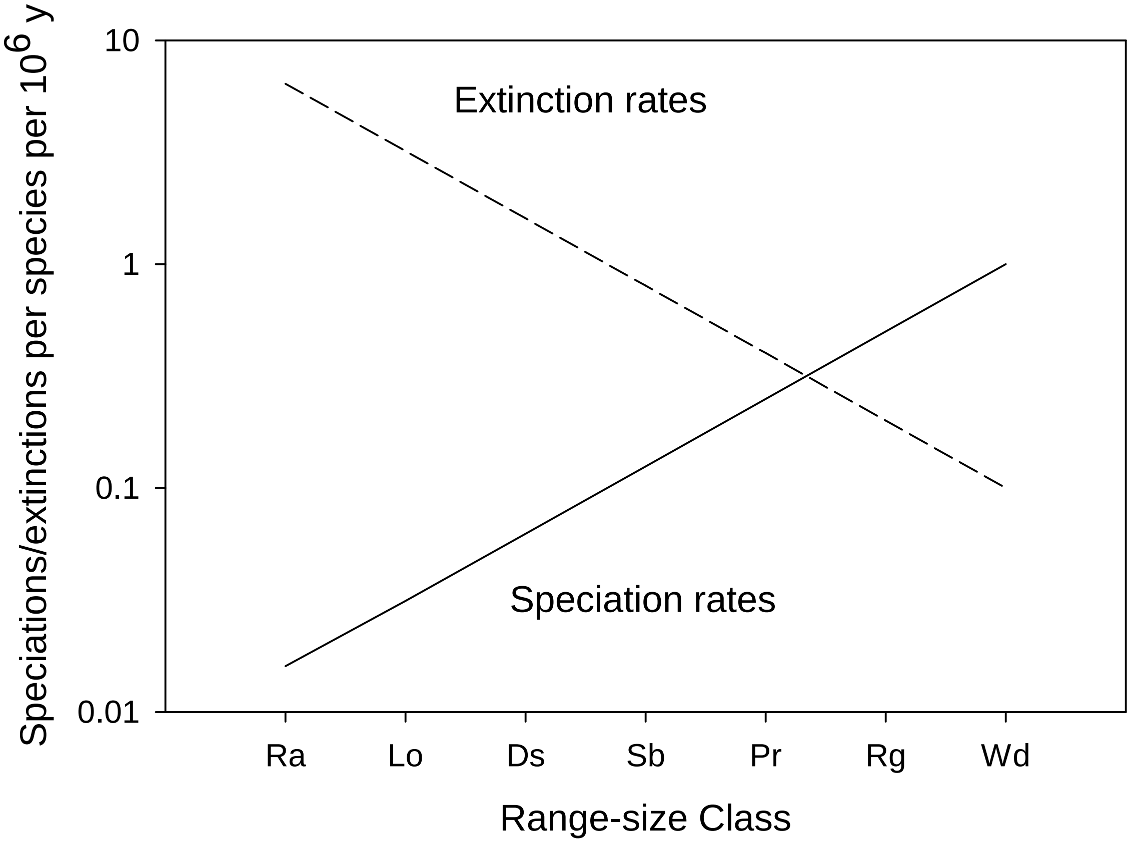
(*IS* = speciations per species per million years)

Group	*IS*	Source
Herbs	1.150	Levin & Wilson (1976)
Shrubs	0.280	Levin & Wilson (1976)
Hardwoods	0.120	Levin & Wilson (1976)
Conifers	0.040	Levin & Wilson (1976)
Dicots	0.730	Nicklas et al. (1983)
Monocots	0.650	Nicklas et al. (1983)
Angiosperms	0.767	Magallon & Sanderson (2001)
Eudicots	0.811	Magallon & Sanderson (2001)
Higher Monocots	0.915	Magallon & Sanderson (2001)
Asterales	2.717	Magallon & Sanderson (2001)
Plants	<0.200?	Coyne & Orr (2004)

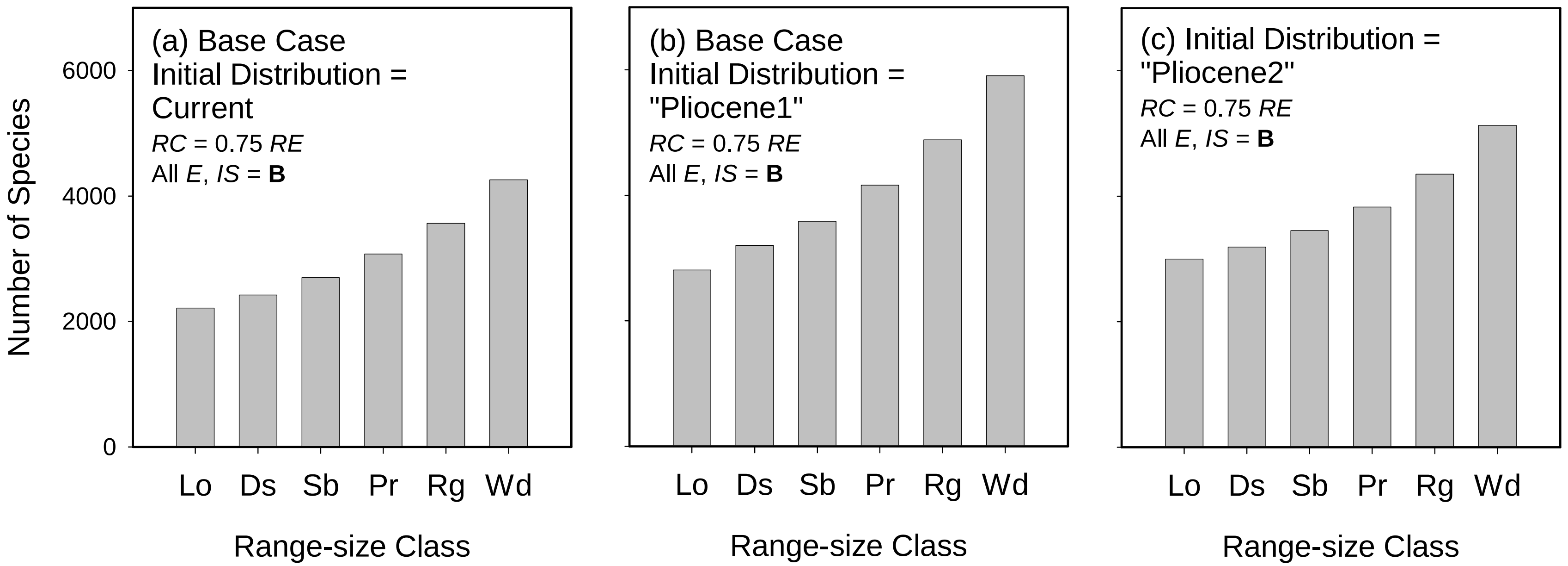
Key assumption: Extinction and speciation rates are a function of range size

- Fossil record contains mostly widespread and abundant species (Jablonski, 1991).
- Extinction and speciation rates from the fossil record therefore apply mostly to these widespread species.
- Extinction rates *increase* with decreasing range size (from widespread to rare species).
- Speciation rates *decrease* with decreasing range size (from widespread to rare species).

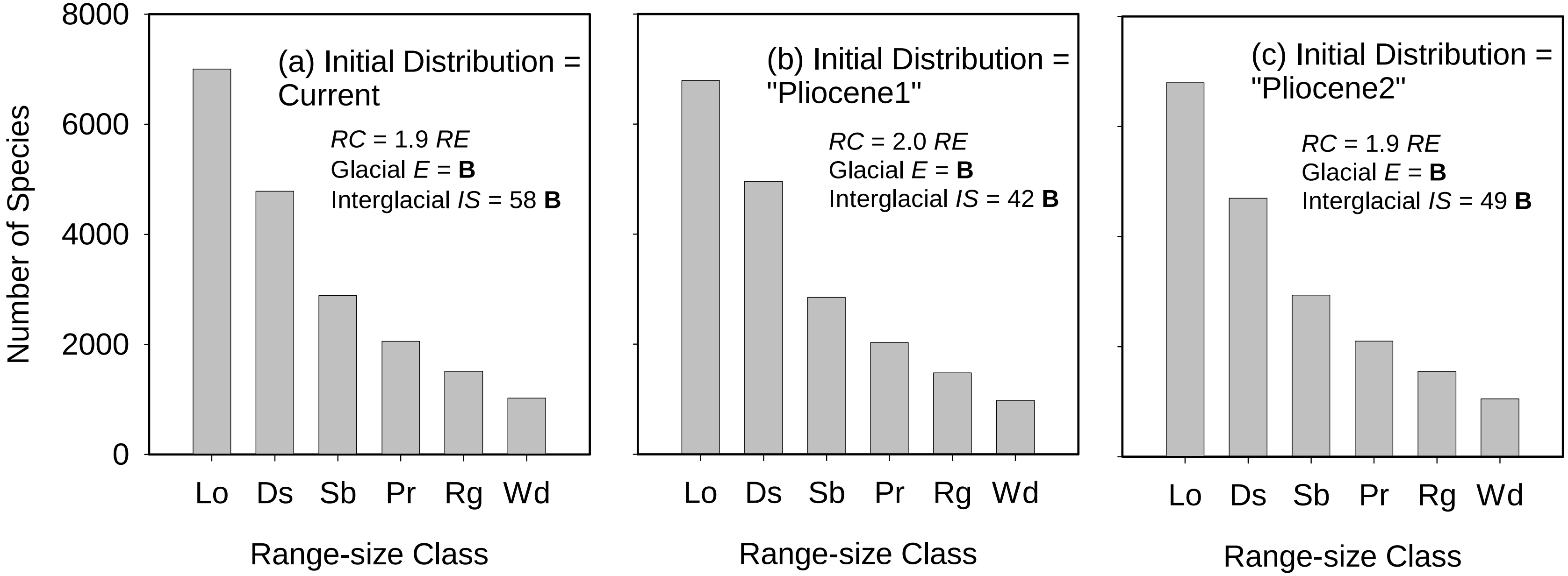
Background Rates of Extinction and Speciation



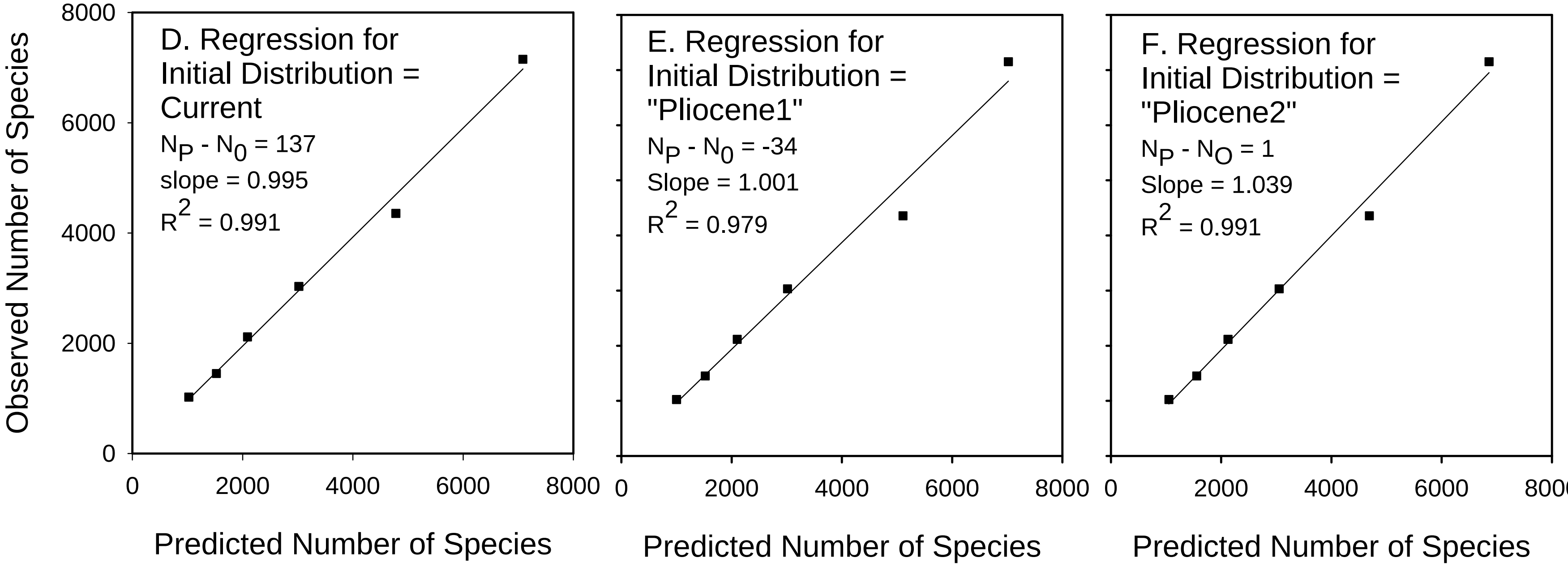
Results 1. Base cases: Frequency Distributions after 20 Glacial-interglacial Cycles



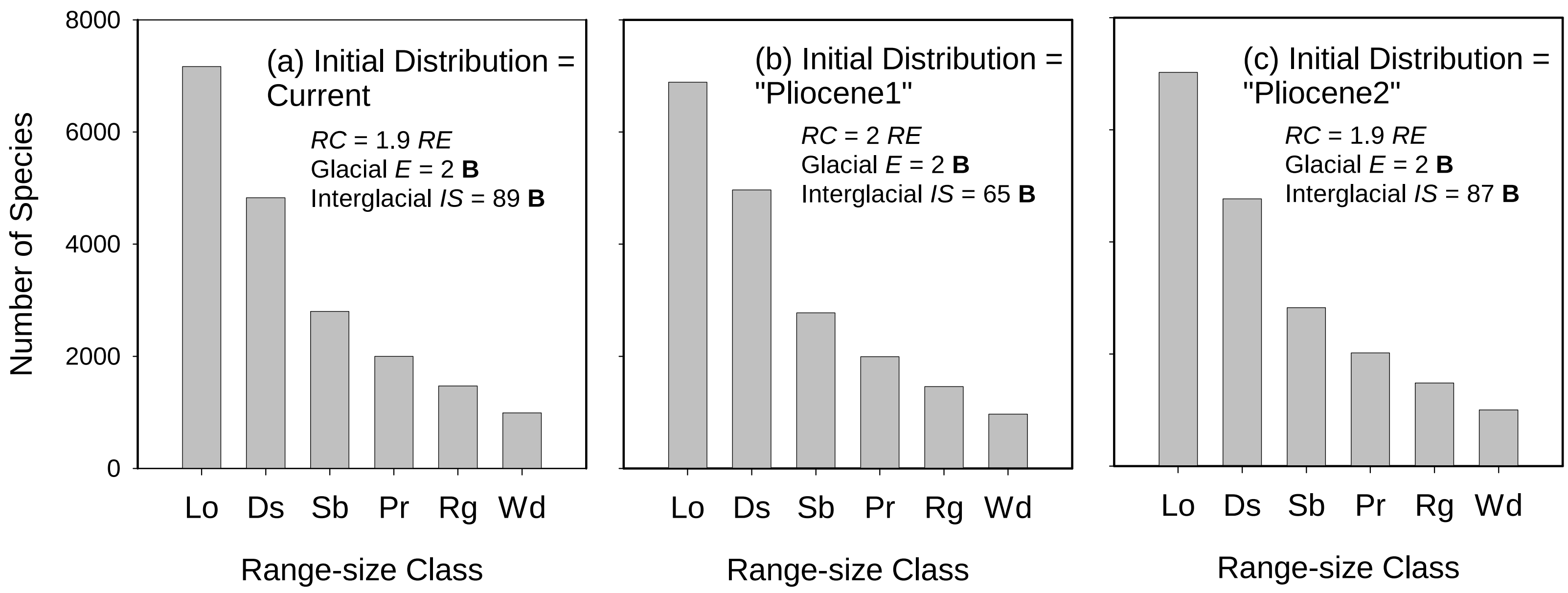
Results 2. Best-case Simulations: Frequency Distributions after 20 Glacial-interglacial Cycles



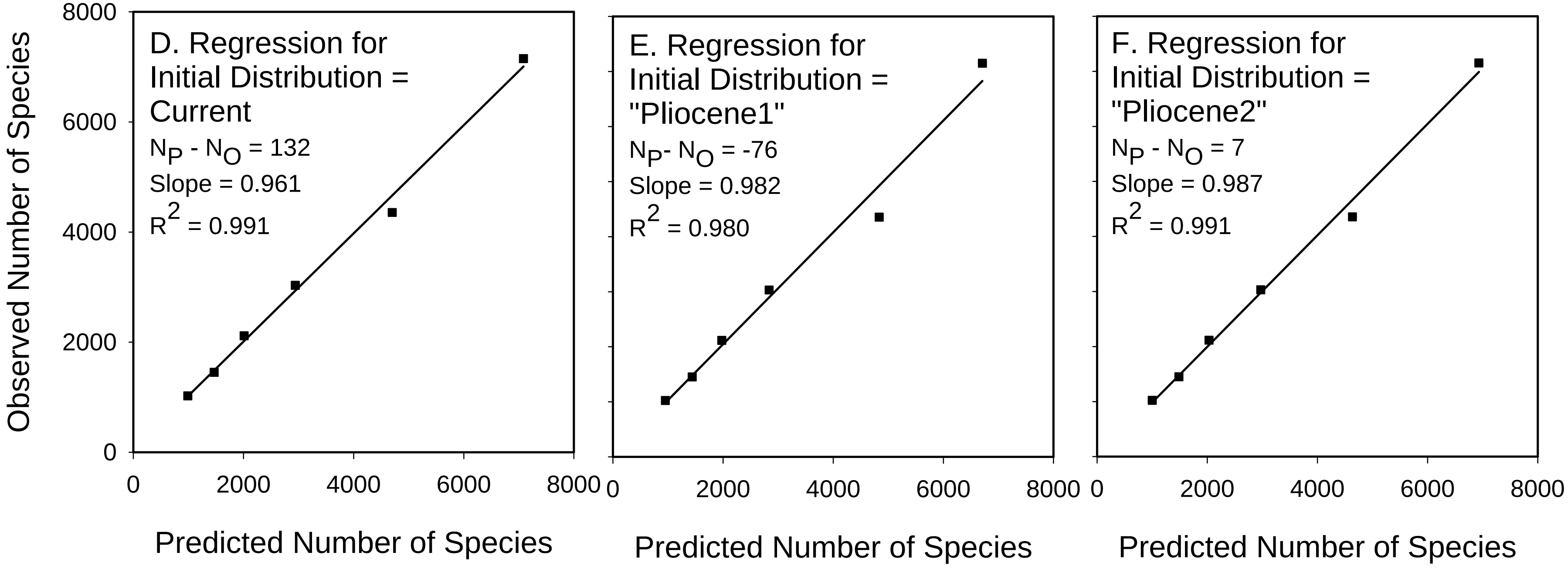
Results 3. Statistical Evaluation of Best-case Simulations



Results 4. Double Glacial Extinction Simulations: Frequency Distributions after 20 Glacial-interglacial Cycles



Results 5. Statistical Evaluations of Double-glacial Extinction Simulations



Results 6. Total Quaternary Extinctions

Quaternary	Extinctions		
Simulations	Current	Pliocene1"	Pliocene2"
Base cases	16917	16760	24979
Best cases	31656	34677	38340
Double G*E*	47574	50037	56537

Results 7. Total Quaternary Speciations

Quaternary	Speciations		
Simulations	Current	Pliocene1"	Pliocene2"
Base cases	2515	4132	2671
Best cases	30798	32324	24979
Double G*E*	45858	49477	41774

Results 8. Holocene Speciations

Holocene	Speciations		
Simulations	Current	Pliocene1"	Pliocene2"
Base cases	70	96	85
Best cases	1502	1057	1303
Double G*E*	2231	1601	2210

Spicer & Chapman
(1990)

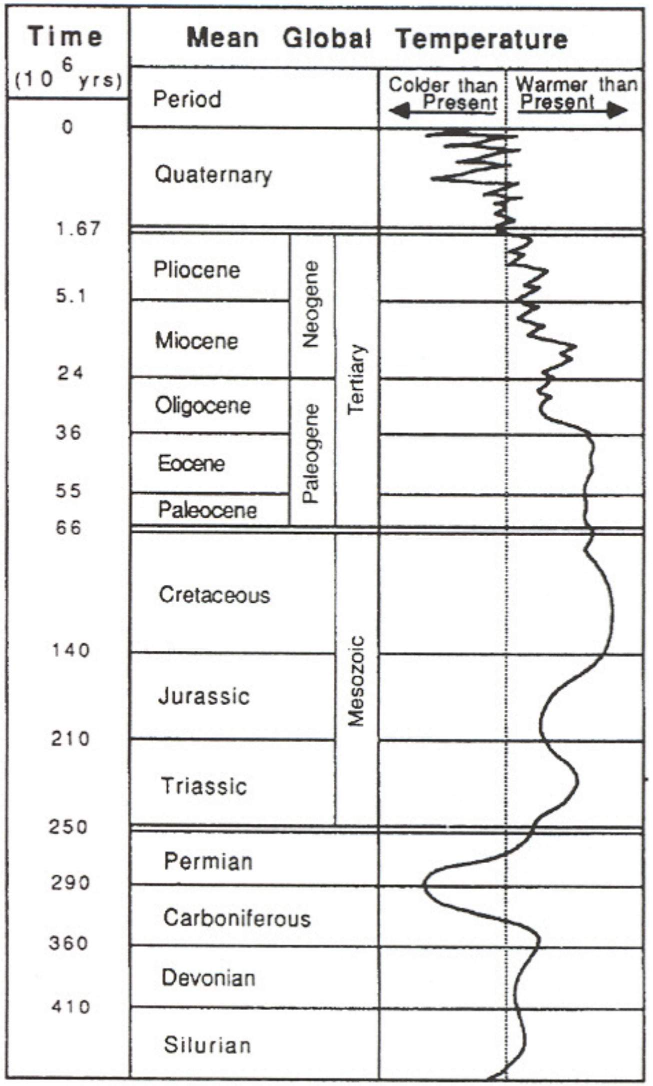


Fig. 1. Relative global temperature curve for the past 440 million years, based on Frakes[1]. Significant glaciation occurred at the Carboniferous–Permian transition and in the Quaternary. For 80% of the last 500 million years the earth has been in a 'greenhouse' mode.

Implications of a more complex Quaternary for the model.

- Parameter values used can be considered as averages. Fluctuations around these mean parameter values may not affect the overall results.

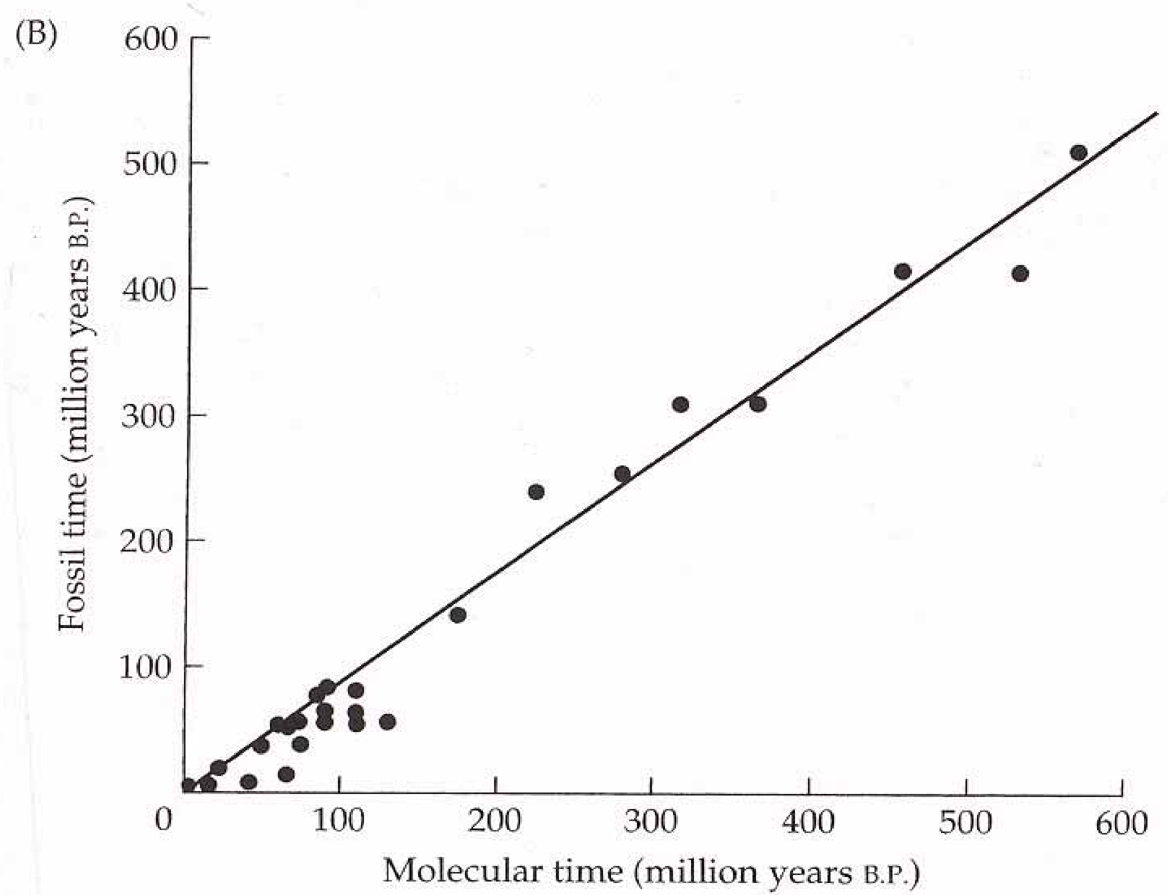
- More intense climatic oscillations in the late Pleistocene would imply even higher extinction and speciation rates in the most recent glacial-interglacial cycles.

- The number of Holocene speciation events would be even higher.

Holocene Speciation: Not a new idea

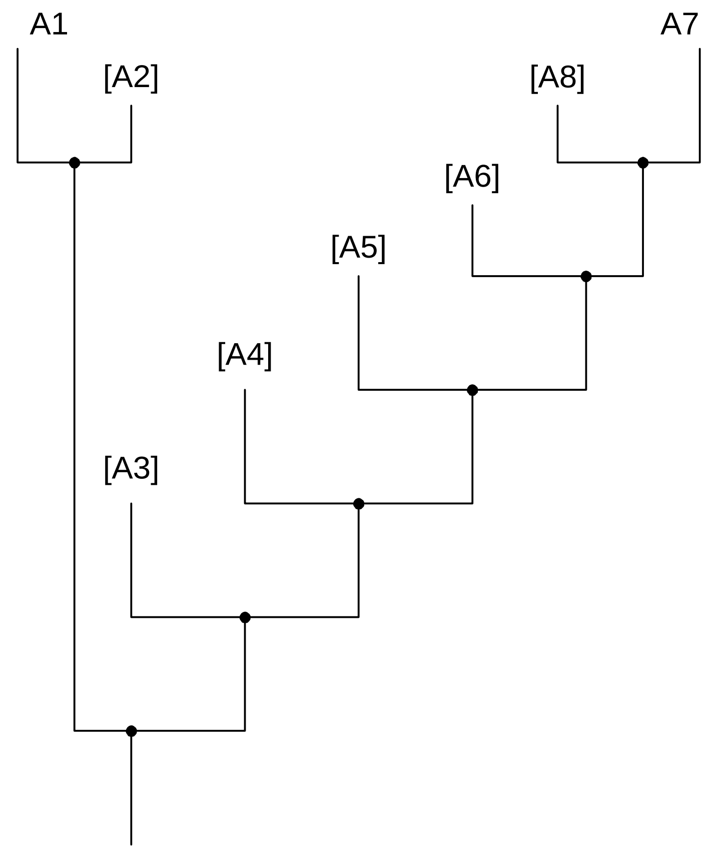
- *Crataegus* (Fernald, 1924)
- *Atriplex* (Stutz, 1978)
- *Arctostaphylos*, *Ceanothus* (Stebbins, 1982)
- California desert ephemerals (*Astragalus*, *Camissonia*, *Chamaesyce*, *Chorizanthe*, *Descurainia*, *Eriogonum*, *Gilia*, *Lupinus*, *Mimulus*, *Nemacladus*, *Phacelia*) (Thorne, 1986)

Molecular data have *not* been interpreted as support for Quaternary speciations. This is a problem.



Can extinctions distort the molecular clock?
Is Pleistocene speciation a “failed paradigm”?

Species A1 and A7 are “pseudosisters”



Conclusions from Modeling

- High ratios of glacial range-contraction rates to interglacial range-expansion rates and high speciation rates are needed to produce characteristic frequency distributions that are highly left-skewed.
- Model simulations suggest that the Quaternary has been a period of high species turnover with tens of thousands of extinctions and speciations in the North American flora.
- One to two thousand or more extant rare and local species in North America likely originated during the Holocene.
- In many clades it must be assumed that there has been significant extinction; many extant species pairs that appear to be sister taxa probably are not.

Conservation Implications

- Periods of global change will result in extinction of many species.
- These models cannot predict *which* species will go extinct; results should not be used as an argument against efforts to prevent extinction due to habit loss, exotic species, exploitation, etc.
- Periods of global change, particularly global warming, are also periods of diversification. Conservation efforts should address conditions that promote speciation as well as extinction. Conditions that promote speciation are habitat preservation and maintaining intraspecific variation in more widespread species.