

History of Historical Biogeography II: Darwin to Models

By Nick Matzke

Common ancestry solved problems

Problems like:

Why no (native) amphibians, terrestrial mammals, earthworms, etc. on remote volcanic islands?

Why do island faunas/floras tend to be a depauperate version of nearby continents?

Why do niches on islands (or isolated continents) seemed to be filled by unusual organisms (unusual, compared to the large continents). (e.g. the kiwi, marsupial lions, etc.)

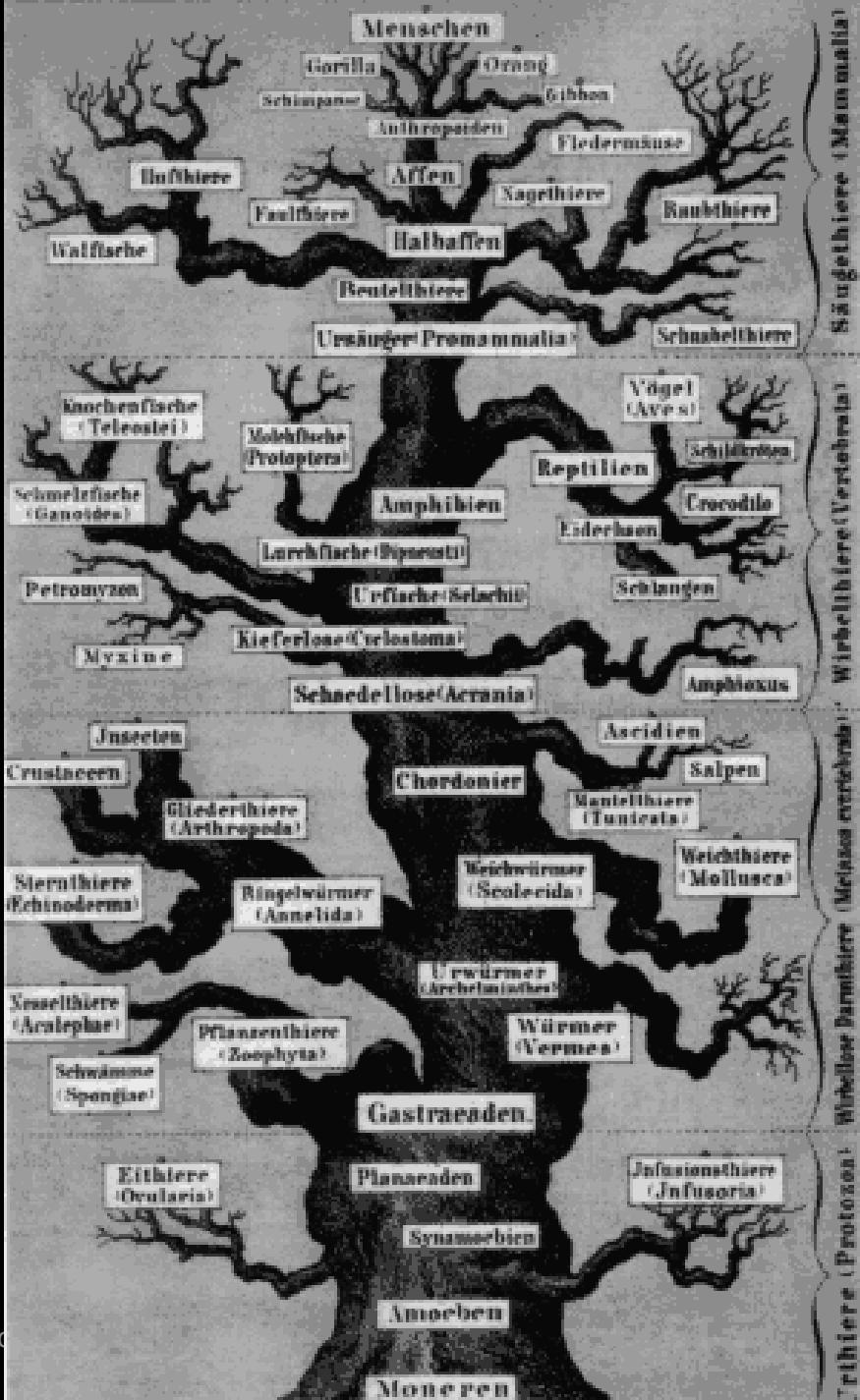
Darwin & Wallace

Geographical similarity due to shared ancestry



Haeckel

Everyone has seen this tree:



Haeckel

Synthetic biogeographical scenario on a map:

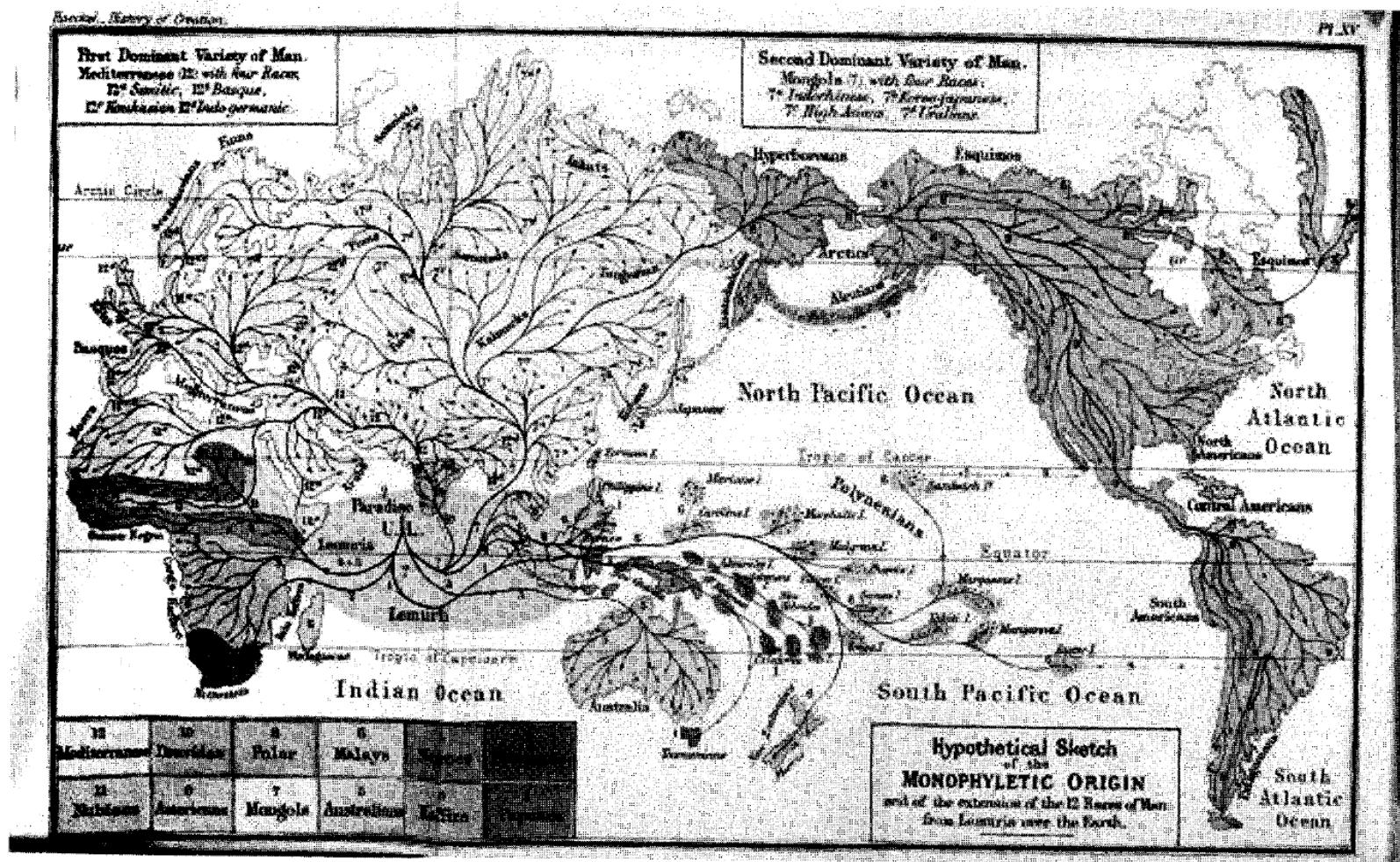
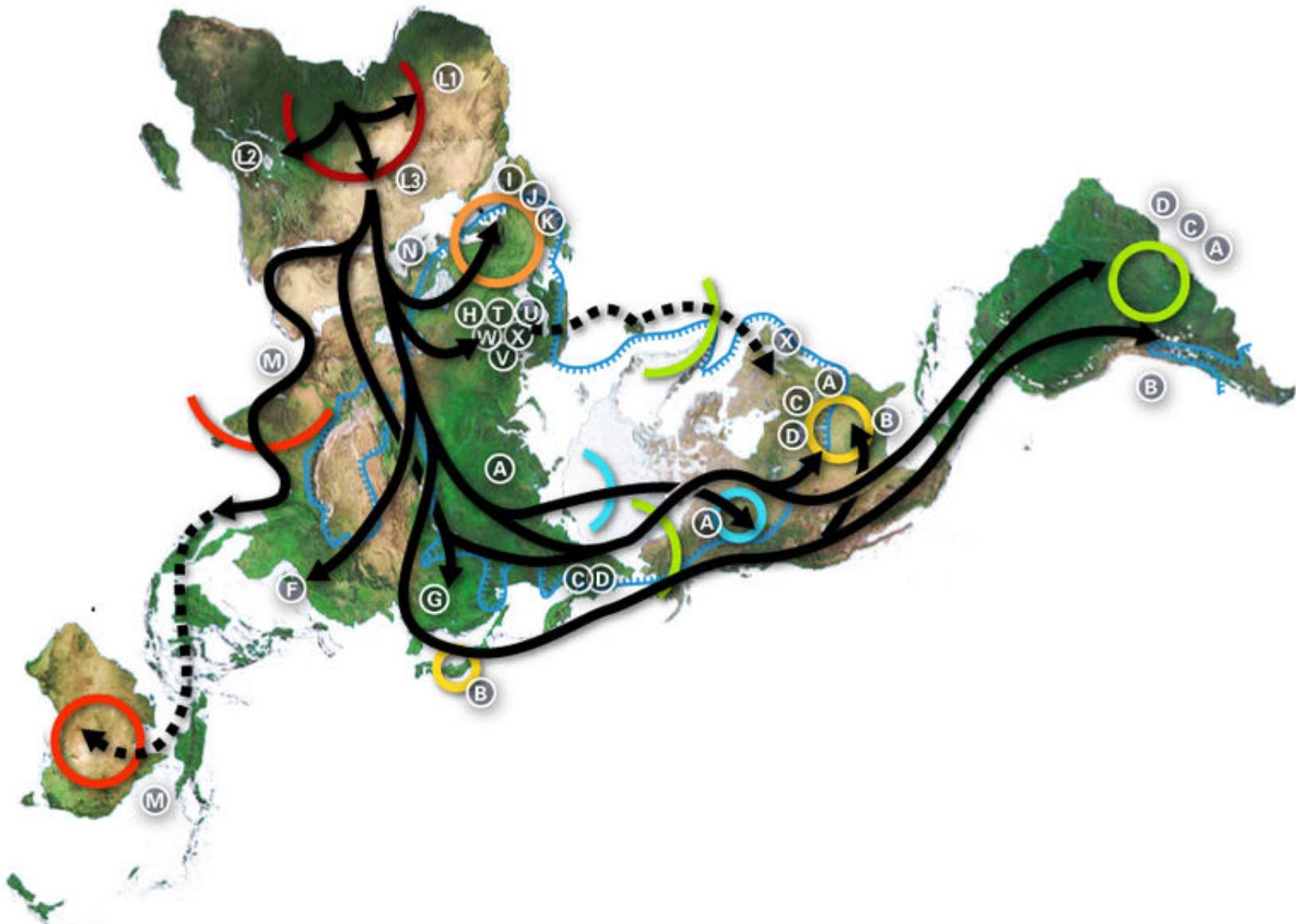
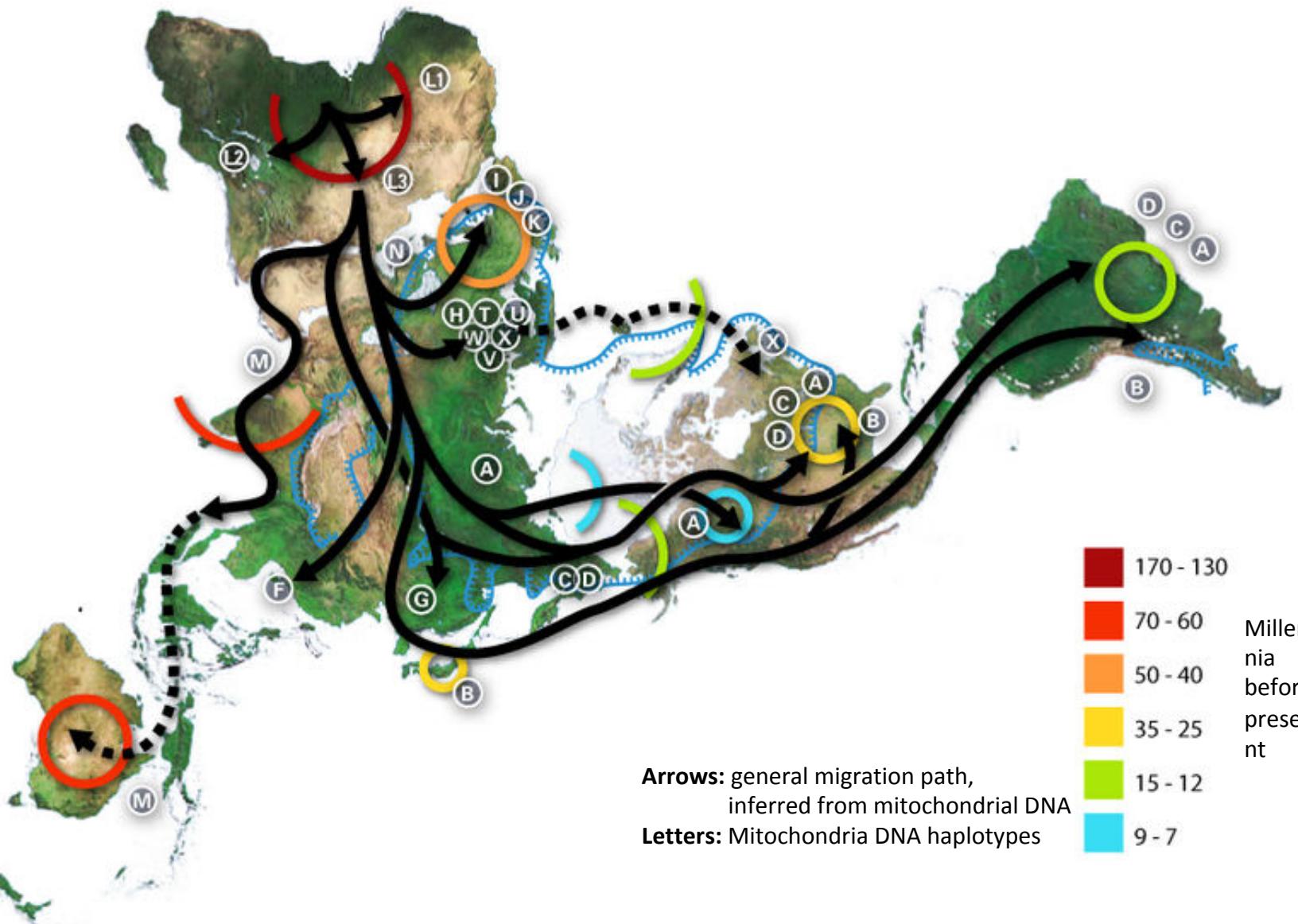


FIGURE 1.9 (See color figure insert following page 76.) Reproduction of *Hypothetical Sketch of the Monophyletic Origin and the Extension of the 12 Races of Man from Lemuria over the Earth* (Haeckel, 1876a, Taf. XV).

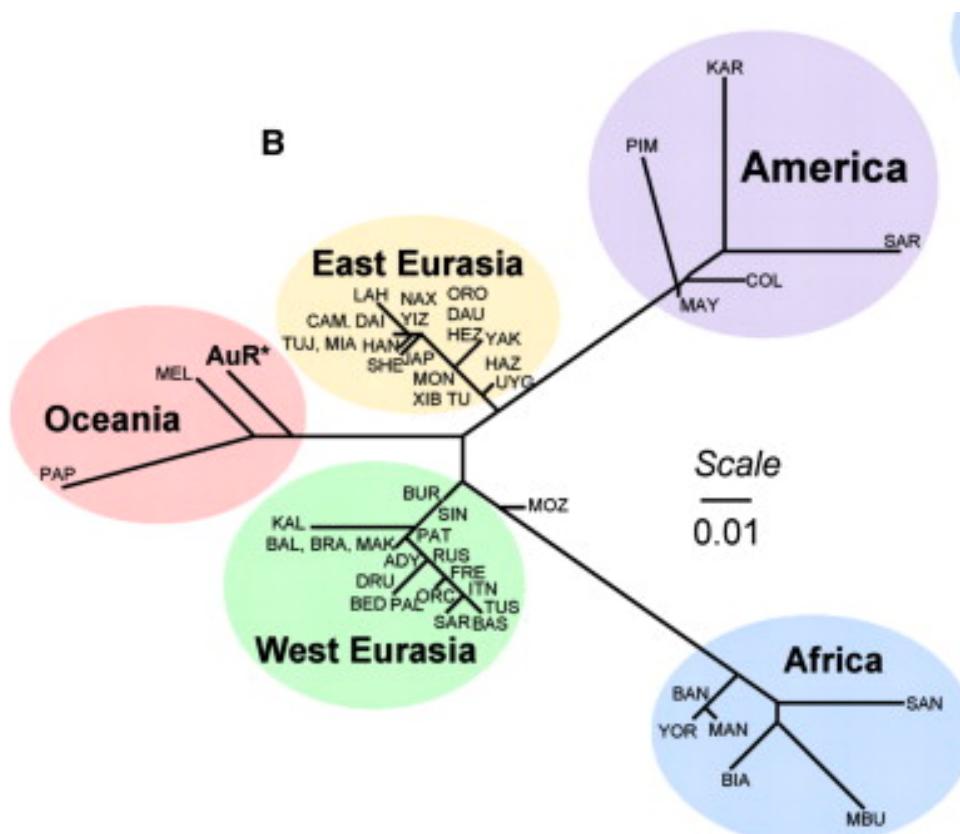
What is historical biogeography?



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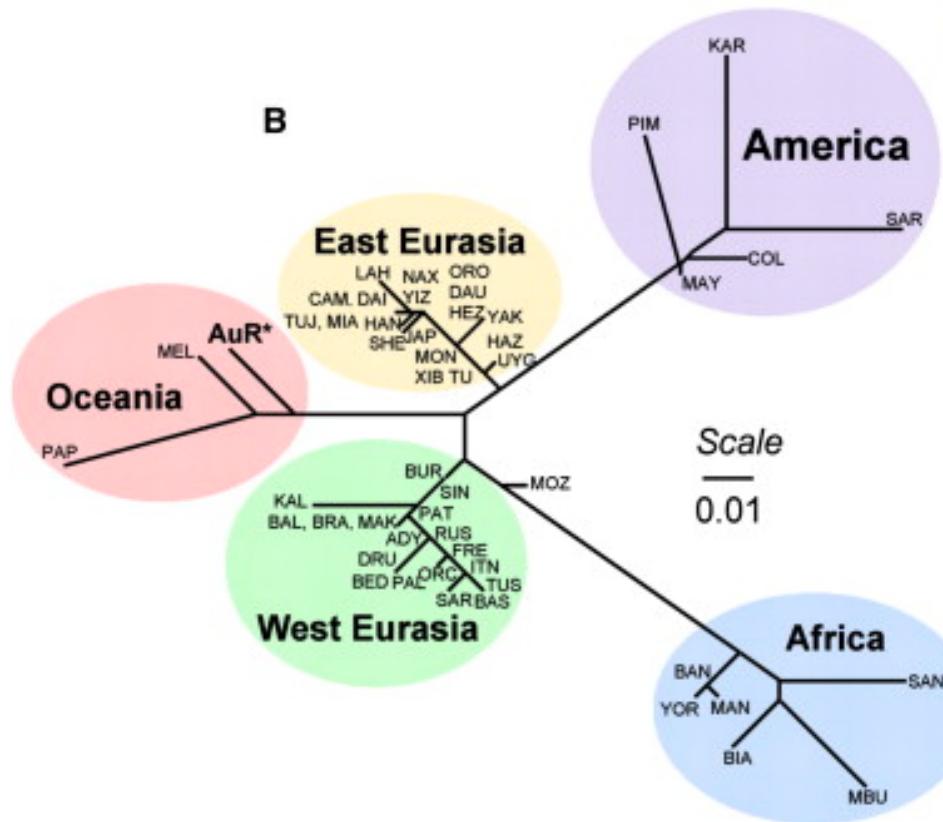
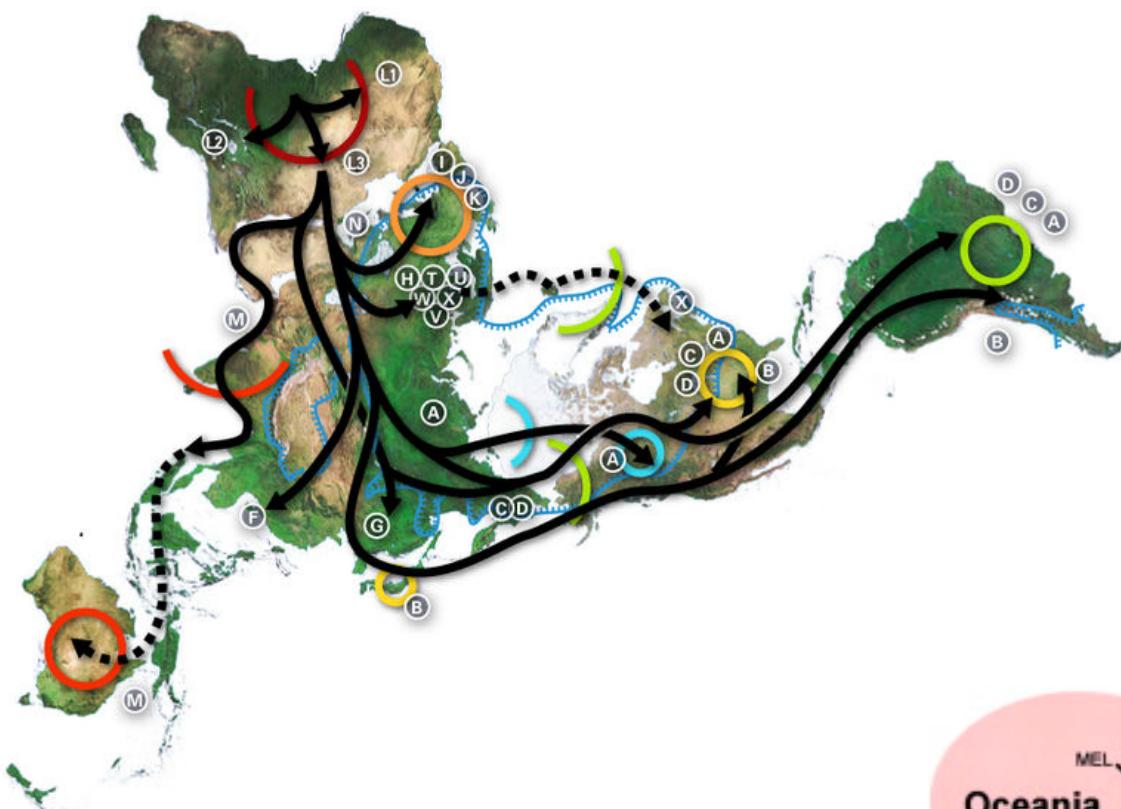


Dendrogram of genetic distances between human populations

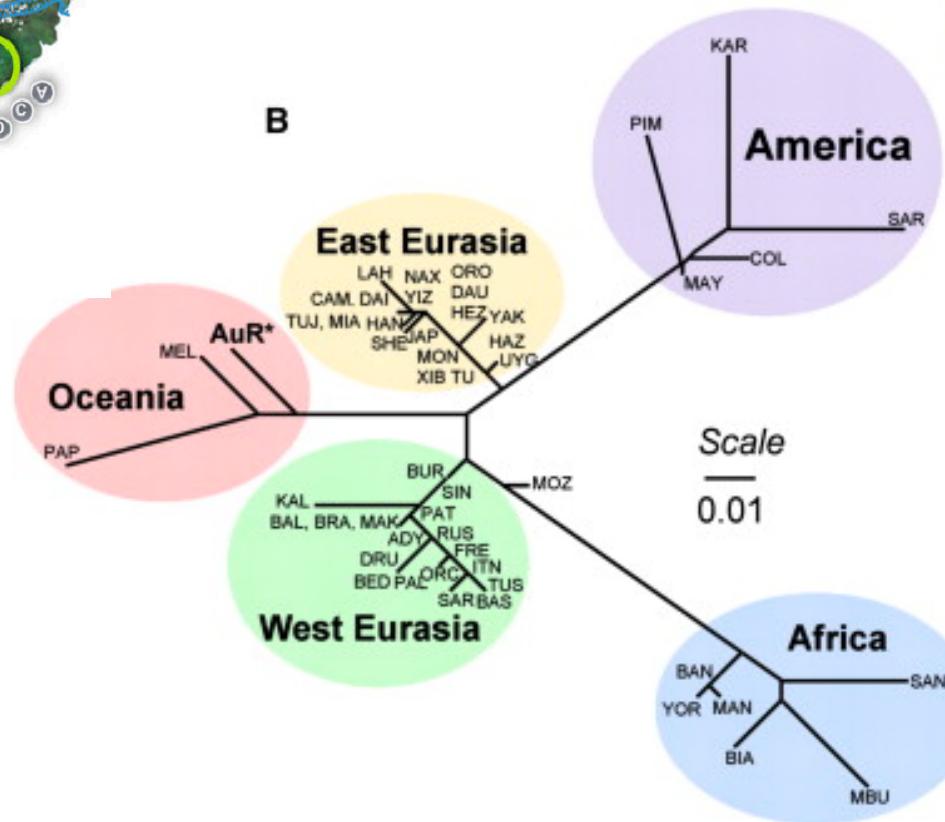
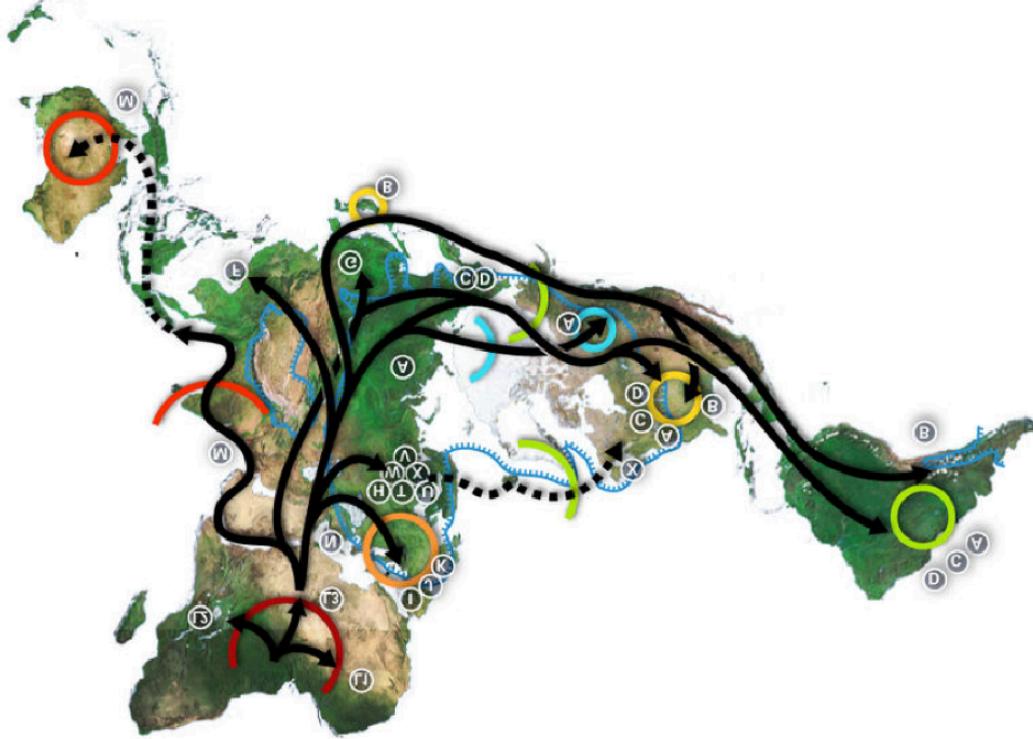
McEvoy et al. (2010), *AJHG*, Figure 1. Unrooted NJ tree of Fst values derived from allele frequencies.

(Note: yes, I know this is a distance tree representing average differences in allele frequencies between populations, not a phylogeny.)

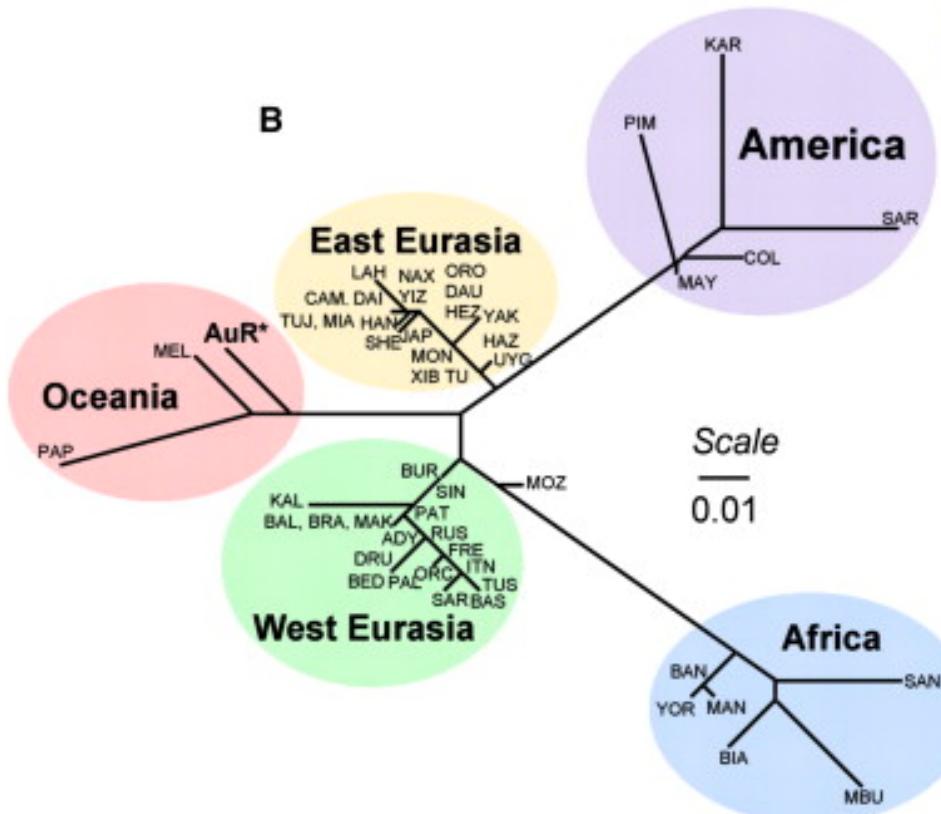
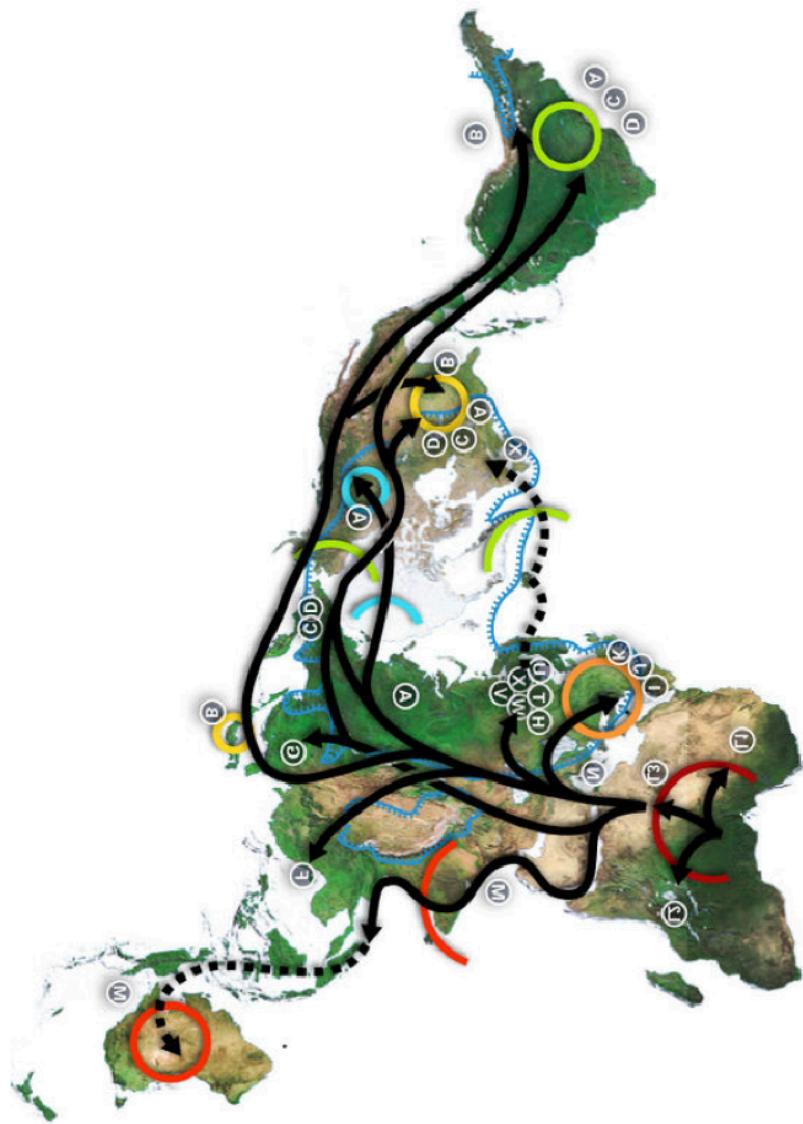
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An Update of Wallace's Zoogeographic Regions of the World

Ben G. Holt,^{1,*} Jean-Philippe Lessard,^{1,*†} Michael K. Borregaard,¹ Susanne A. Fritz,^{1,2} Miguel B. Araújo,^{1,3,4} Dimitar Dimitrov,⁵ Pierre-Henri Fabre,⁵ Catherine H. Graham,⁶ Gary R. Graves,^{1,7} Knud A. Jønsson,⁵ David Nogués-Bravo,¹ Zhiheng Wang,¹ Robert J. Whittaker,^{1,8} Jon Fjeldså,⁵ Carsten Rahbek¹

Modern attempts to produce biogeographic maps focus on the distribution of species, and the maps are typically drawn without phylogenetic considerations. Here, we generate a global map of zoogeographic regions by combining data on the distributions and phylogenetic relationships of 21,037 species of amphibians, birds, and mammals. We identify 20 distinct zoogeographic regions, which are grouped into 11 larger realms. We document the lack of support for several regions previously defined based on distributional data and show that spatial turnover in the phylogenetic composition of vertebrate assemblages is higher in the Southern than in the Northern Hemisphere. We further show that the integration of phylogenetic information provides valuable insight on historical relationships among regions, permitting the identification of evolutionarily unique regions of the world.

Biogeographic and bioclimatic regions are the fundamental units of comparison in many broad-scale ecological and evolutionary studies (1, 2) and provide an essential tool

for conservation planning (3, 4). In 1876, Alfred Russel Wallace published the first map of global terrestrial zoogeographic regions (5), which later became the cornerstone of modern biogeography

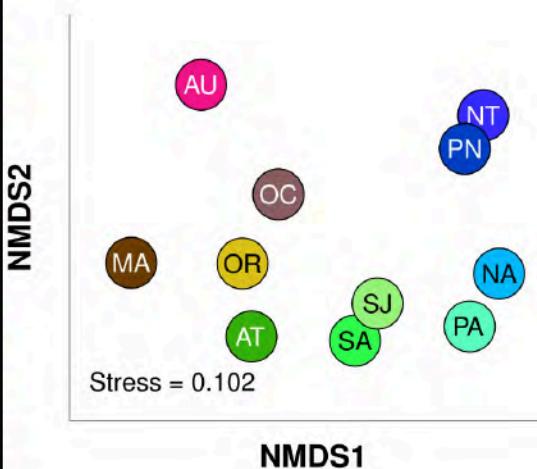


Fig. S1. Map, dendrogram and NMDS of cross-taxon zoogeographic realms based on phylo-distributional data for amphibian, bird and non-marine mammal species of the world. The

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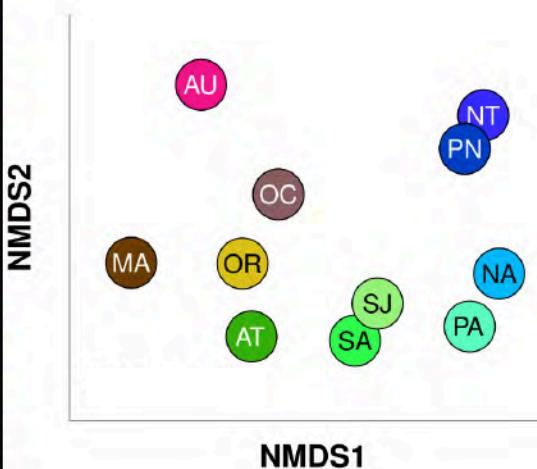


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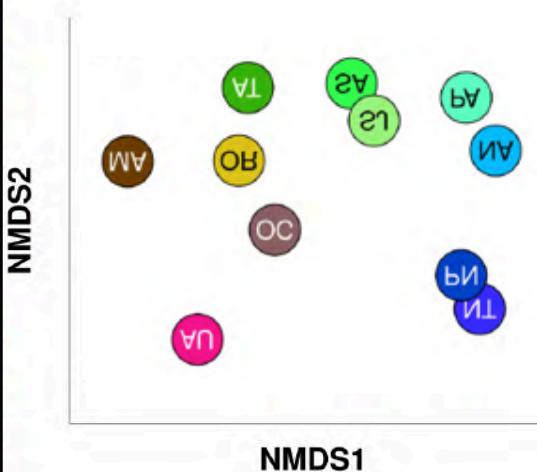


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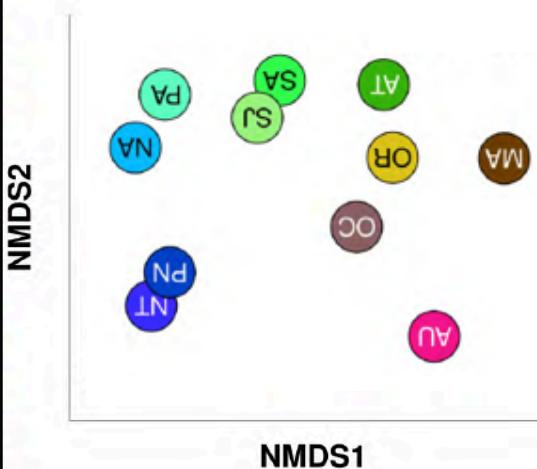


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1859-1950s: “Darwinian” biogeography

Centers of distribution/endemism

- Most diversity = center of origin

Delineation of “biogeographical provinces”

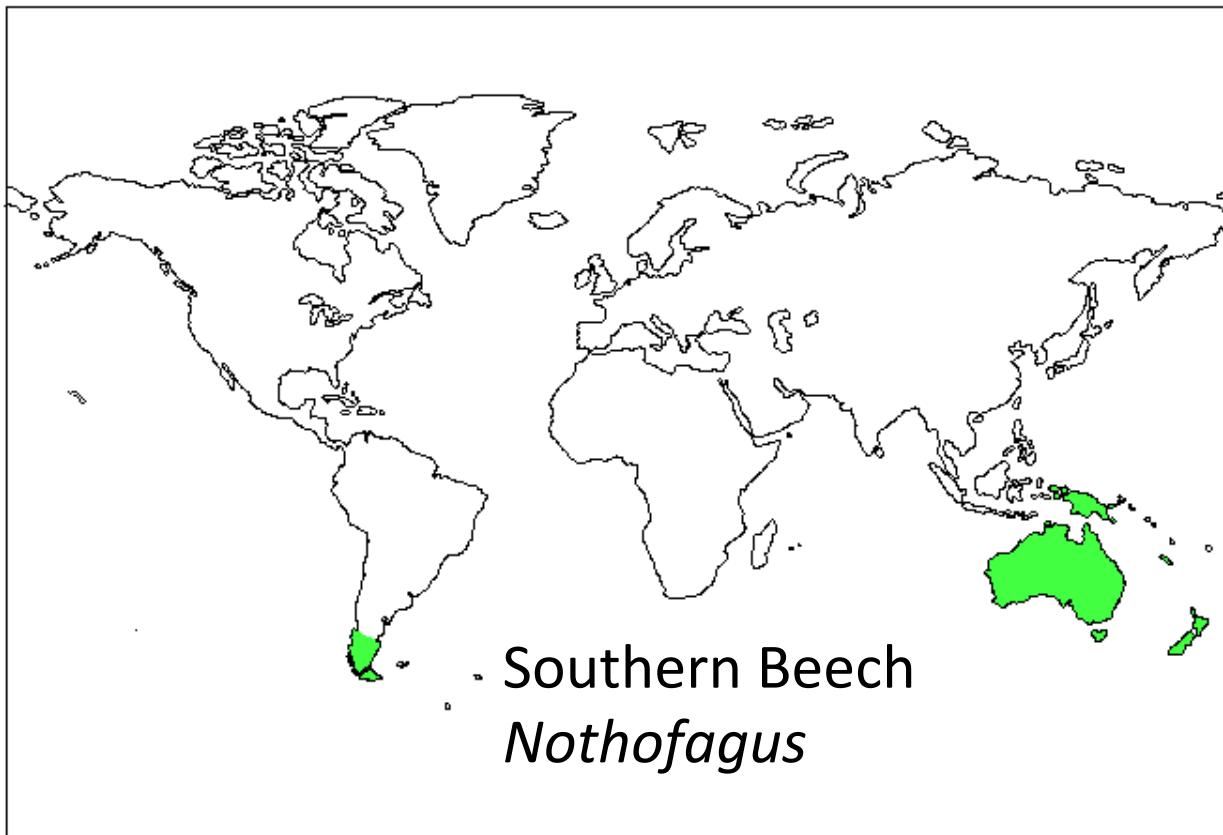
Disjunct patterns:

- Dispersal
- Land bridges

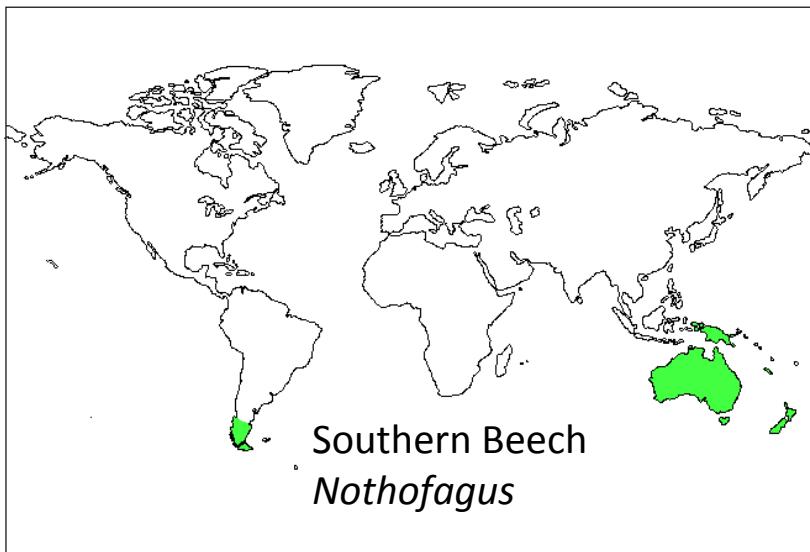
Develop a “synthetic scenario” (i.e. a story)

Darwin to Lyell: land bridges were being created
“as easy as a cook does pancakes.”

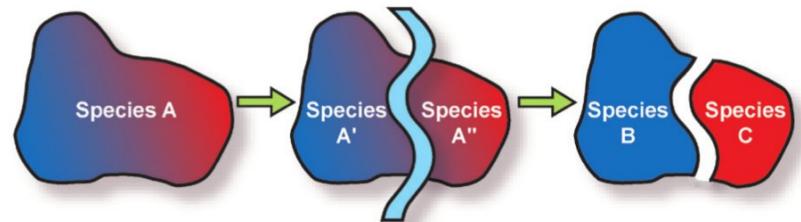
Evolution solved one biogeographical problem, but created new puzzles



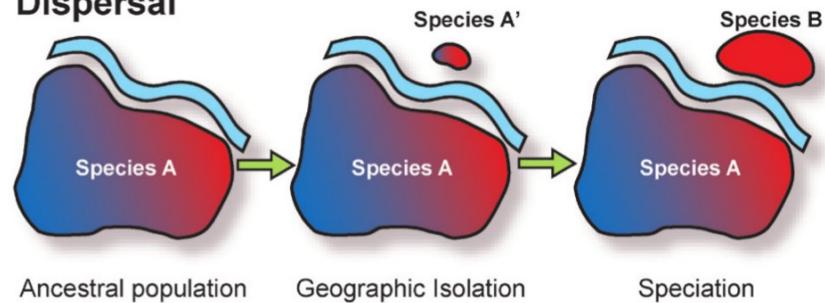
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Vicariance



Dispersal



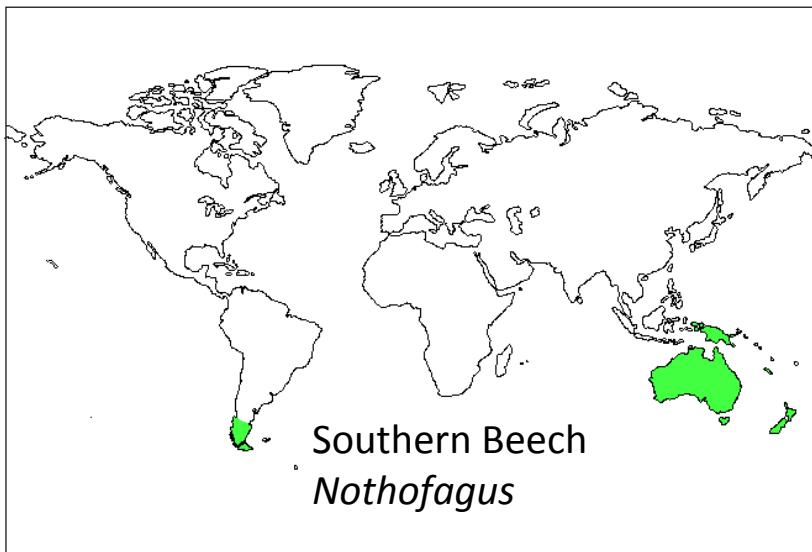
Ancestral population

Geographic Isolation

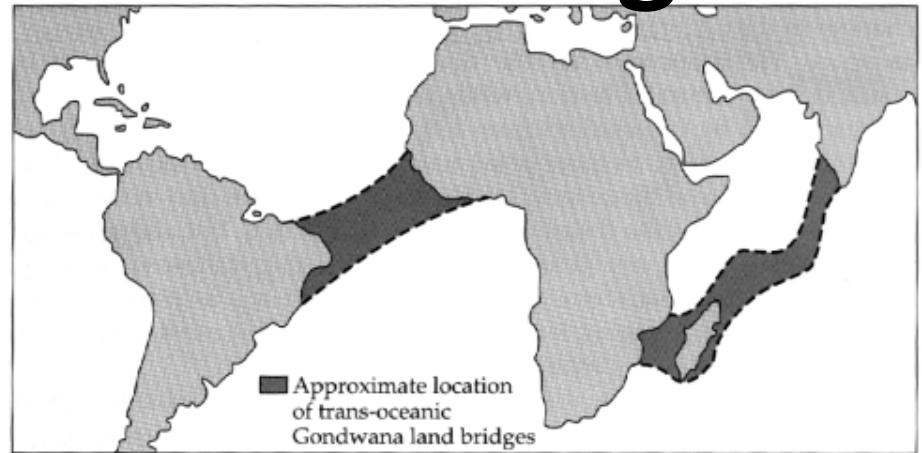
Speciation

Figure 2. Geography of allopatric speciation modes. In vicariance, the ancestral population (Species A) is passively divided by a geographic barrier. Incipient species (Species A' and A'') form during geographic isolation and later diverge to become new species (Species B and C). In dispersal, a subpopulation of the ancestral species (Species A) actively migrates across a geographic barrier to form an incipient species (Species A'), which later diverges to become a new species (Species B).

Evolution solved one biogeographical problem, but created new puzzles



Land bridges?



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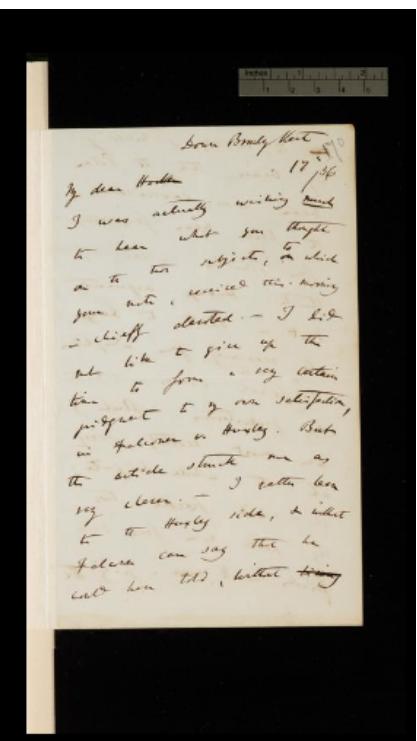
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Darwin, C. R. to Hooker, J. D.

17–18 [June 1856]

Letter 1904



Talking of eocene geology, I got so wrath about the Atlantic continent, more especially from a note from Woodward (who has published a **capital** book on shells) who does not seem to doubt that *every island* in Pacific & Atlantic are the remains of continents, submerged within period of existing species; that I fairly exploded & wrote to Lyell to protest & summed up all the continents created of late years by Forbes, (the head *sinner!*) *yourself*, Wollaston, & Woodward & a pretty nice little extension of land they make altogether! ^{f9} I am fairly *rabid* on the question & therefore, if not wrong already, am pretty sure to become so.

I have just reread your note & it seems to me that there is great justness in your remarks on Huxley & the general question, being discussed as it has been discussed.— ^{f10}

I have enjoyed your note much

Adios. | C. Darwin

P.S | 18th Lyell has written me a **capital** letter on your side, ^{f11} which ought to upset me entirely, but I cannot say it does quite.— Though I must try & cease being rabid & try to feel humble, & allow you all to make continents, as easily as a Cook does pancakes.—

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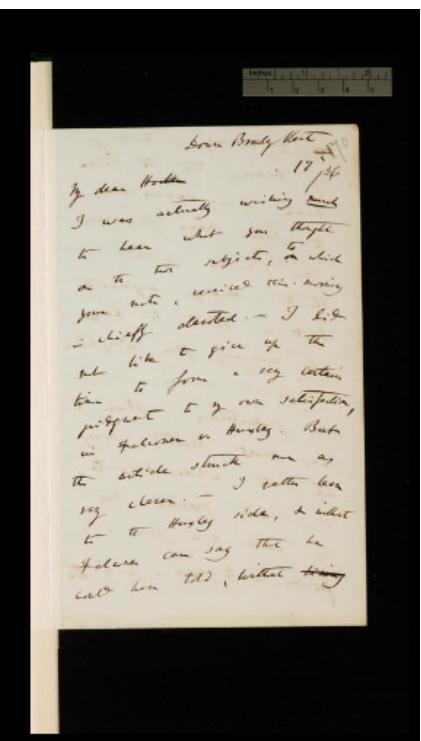
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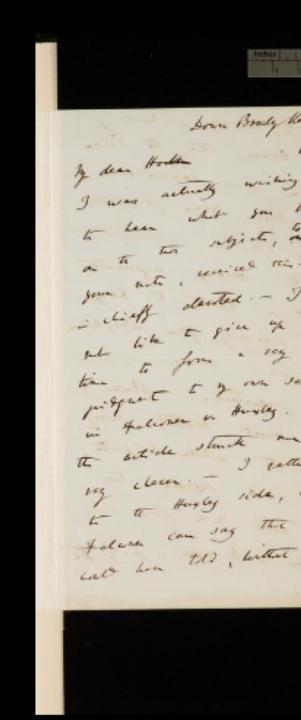
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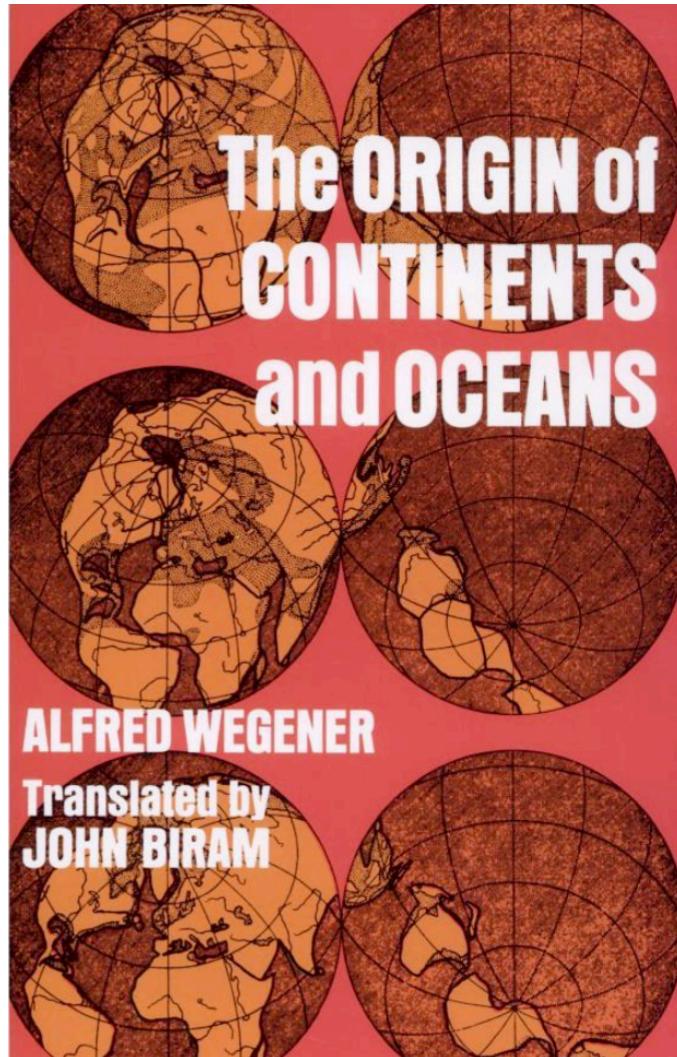


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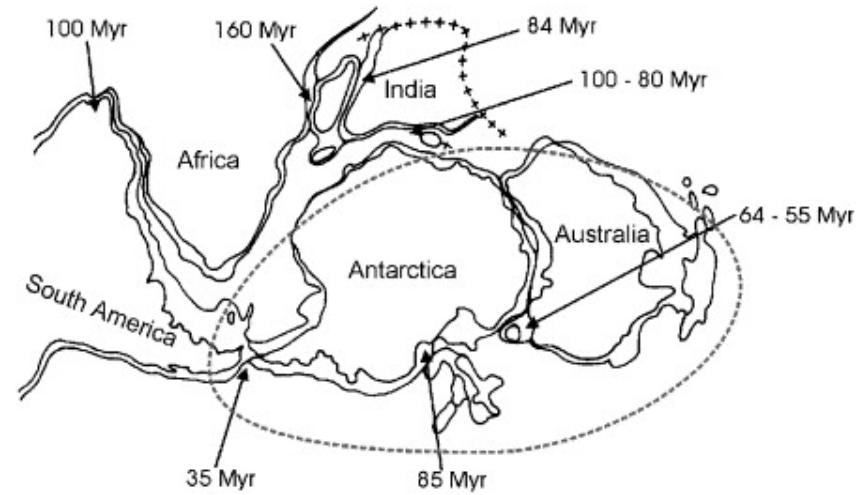
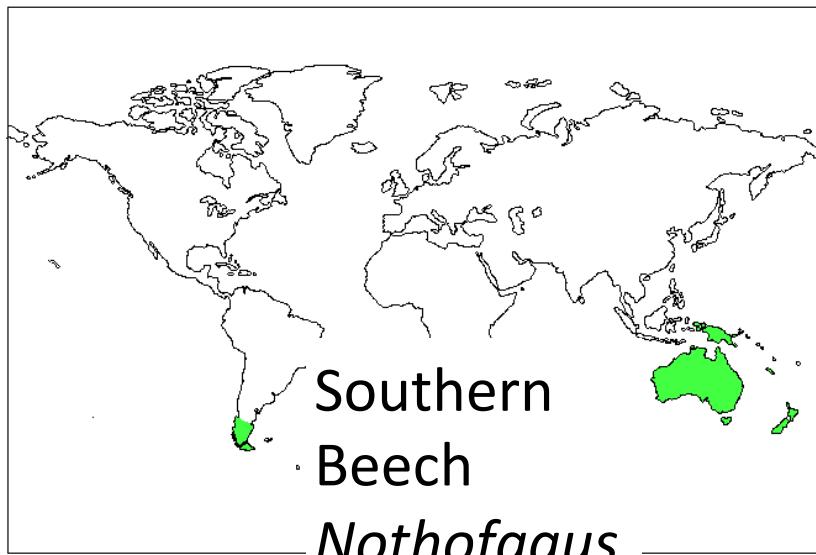
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Wegener, continental drift



	AMERIKANISCHE	SÜDPAZIFISCHE	NORDPAZIFISCHE	ARABISCHE	EUROAFRIISCHE	EURASISCHE	EURASBRÜCKE
Rhaet	+ -	+ -	+ -	+ -	+ -	+ -	+ -
Lias	2	1 2	2	2	3	3	
Unter-Dogger	6	1 5	4 2	2 1	4	4	
Ober-Dogger	4	1 5	3 1	2	3	3	4
Unter-Kreide	3	1 3	1 2	2	3	5	5
Ältere Unter-Kreide	8	1 6	7	6	6	6	7
Jüngere Unter-Kreide	1	1 1	2	1	1	1	1
Mittel-Kreide	3	2 5	2 5	6	6	6	3 3
Ober-Kreide	4	2 7	4 6	8	8	8	8 1
Unteres Eozän	2	1 5	7 1	1 5	6	6	3 5
Oberes Eozän	5	5 7	1	6	6	6	6
Oligozän	6	4 7		4	4	4	5
Miozän	2	6	7 1	3 4	7	6	1
Pliozän	4	3 3	1	3	1 2	3	
Quartär	4	3 3	3	1 2	4		

Plate tectonics led many to favor vicariance

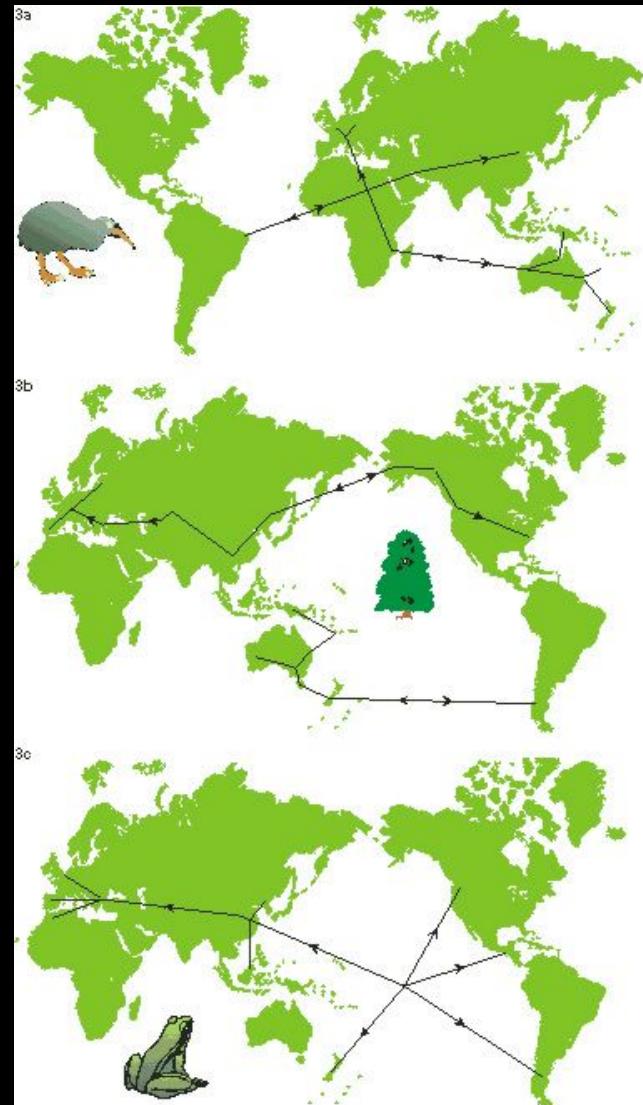


Posadasa et al. (2006). "Historical biogeography: A review of its basic concepts and critical issues." *Journal of Arid Environments*, 66(3), 389–403.

1950s-1980s: panbiogeography

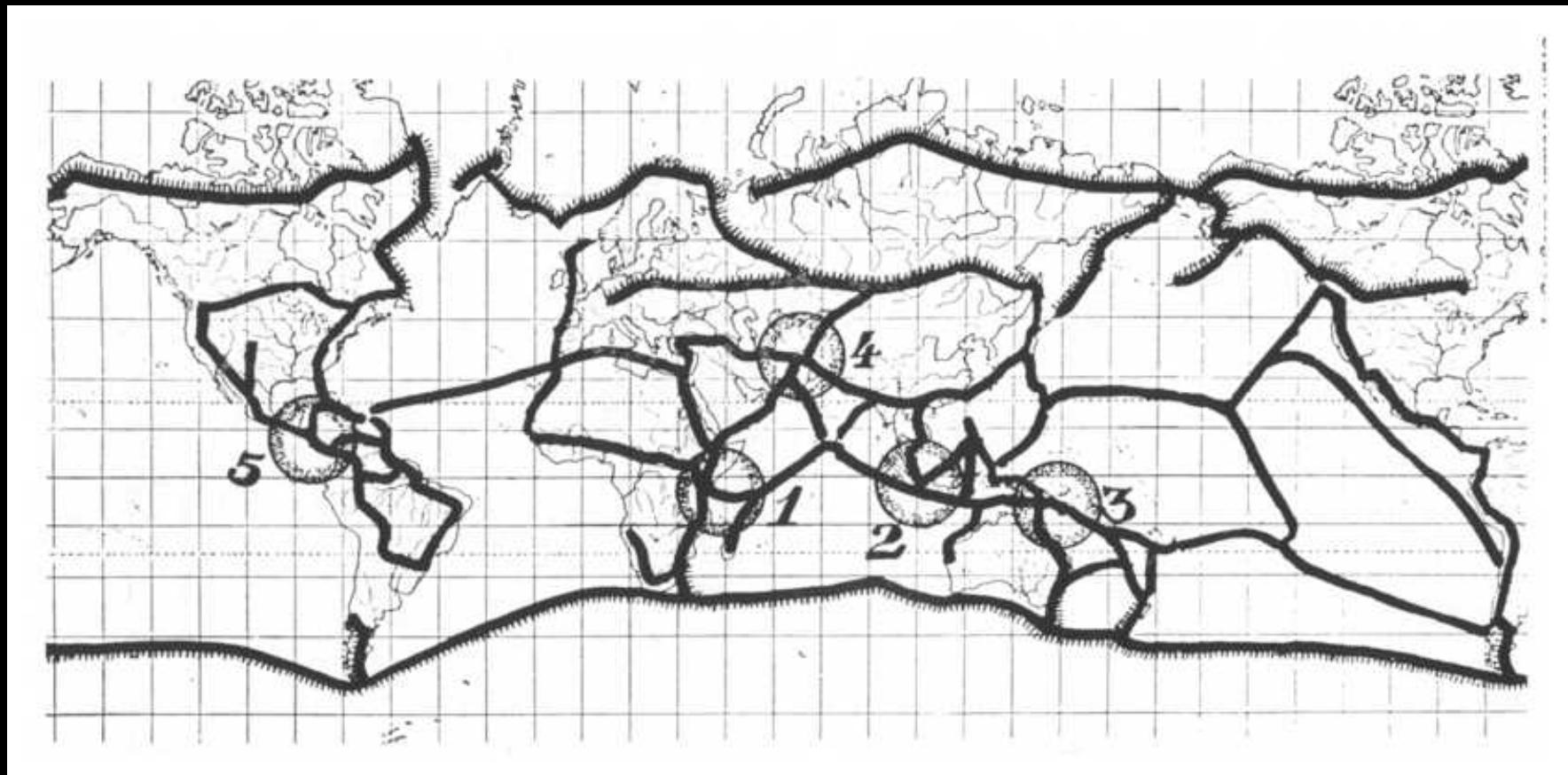
Look for “tracks” connecting members of a taxon; look for shared patterns in tracks

- Leon Croizat
- anti-dispersalist
- focused on pattern rather than process
- polemical & ideological
- taxonomy- rather than phylogenetically based; huge polyphyly/paraphyly problems
- seen by some to support plate tectonics



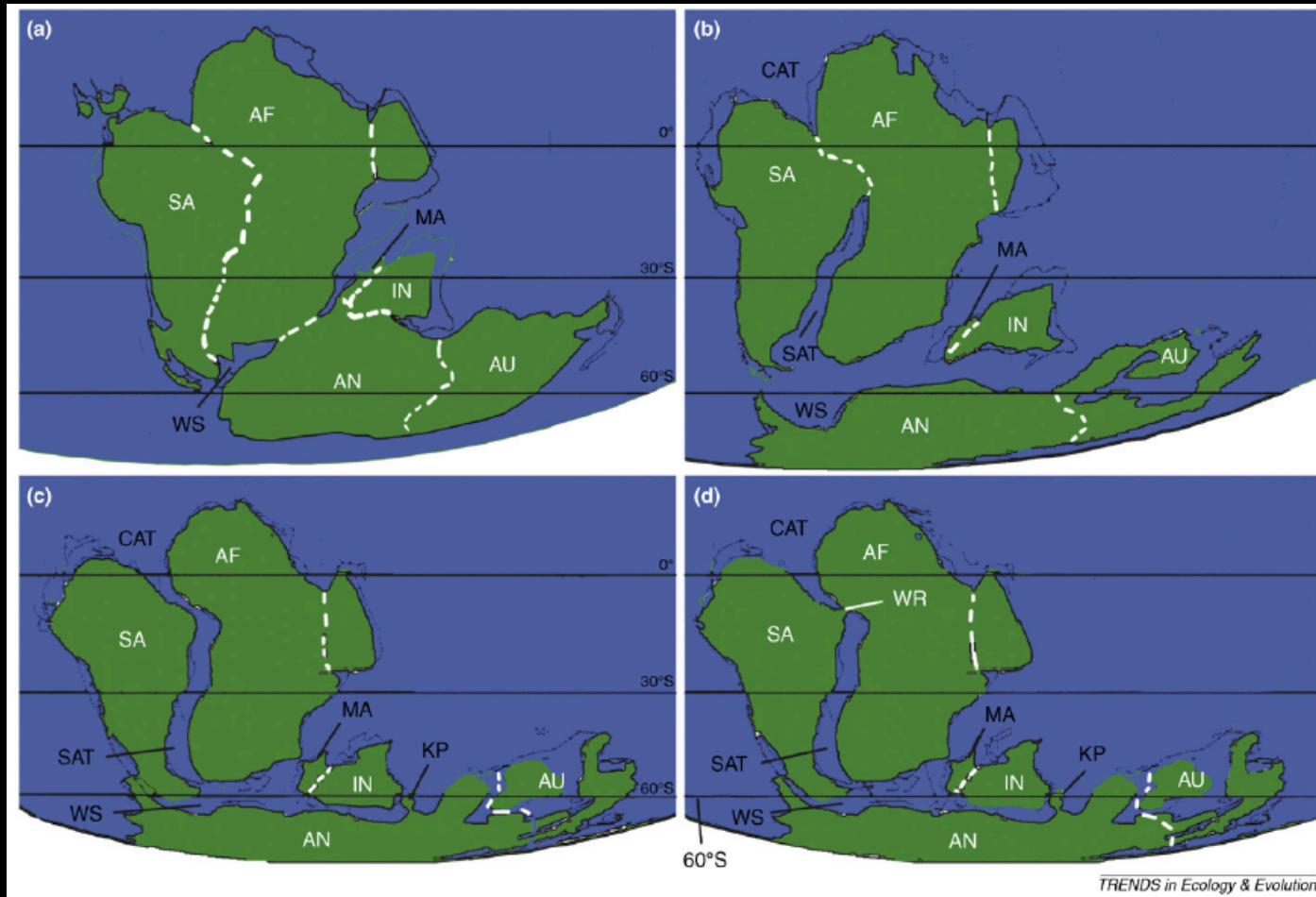
1950s-1980s: panbiogeography

Methodology unclear...



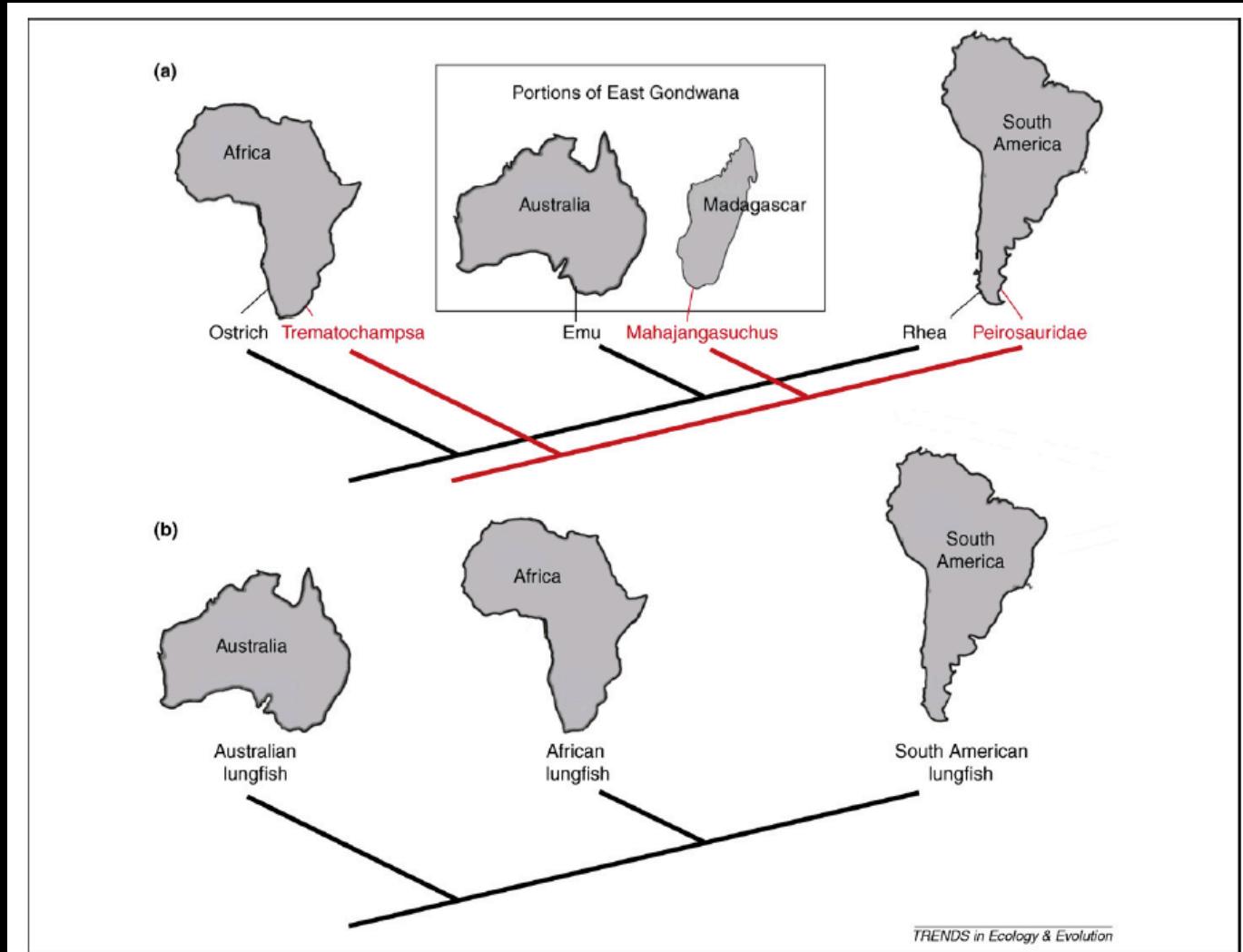
Croizat's summary diagram of global tracks from his (1958) *Panbiogeography*

1960s-1990s: plate tectonics & cladistic biogeography

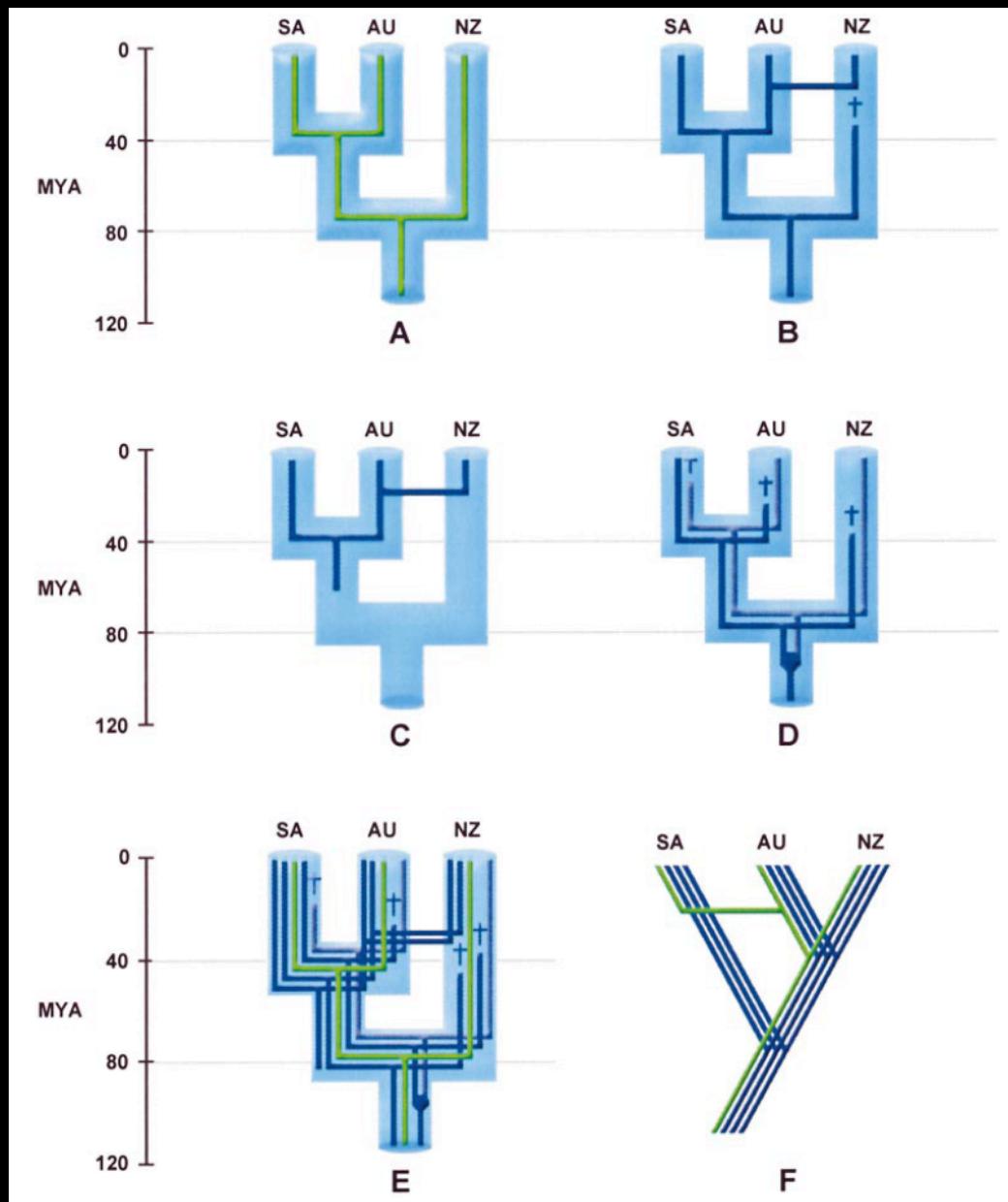


Different scenarios for breakup of Gondwanaland

1960s-1990s: plate tectonics & cladistic biogeography



1960s-1990s: plate tectonics & cladistic biogeography



Donoghue & Moore (2003)

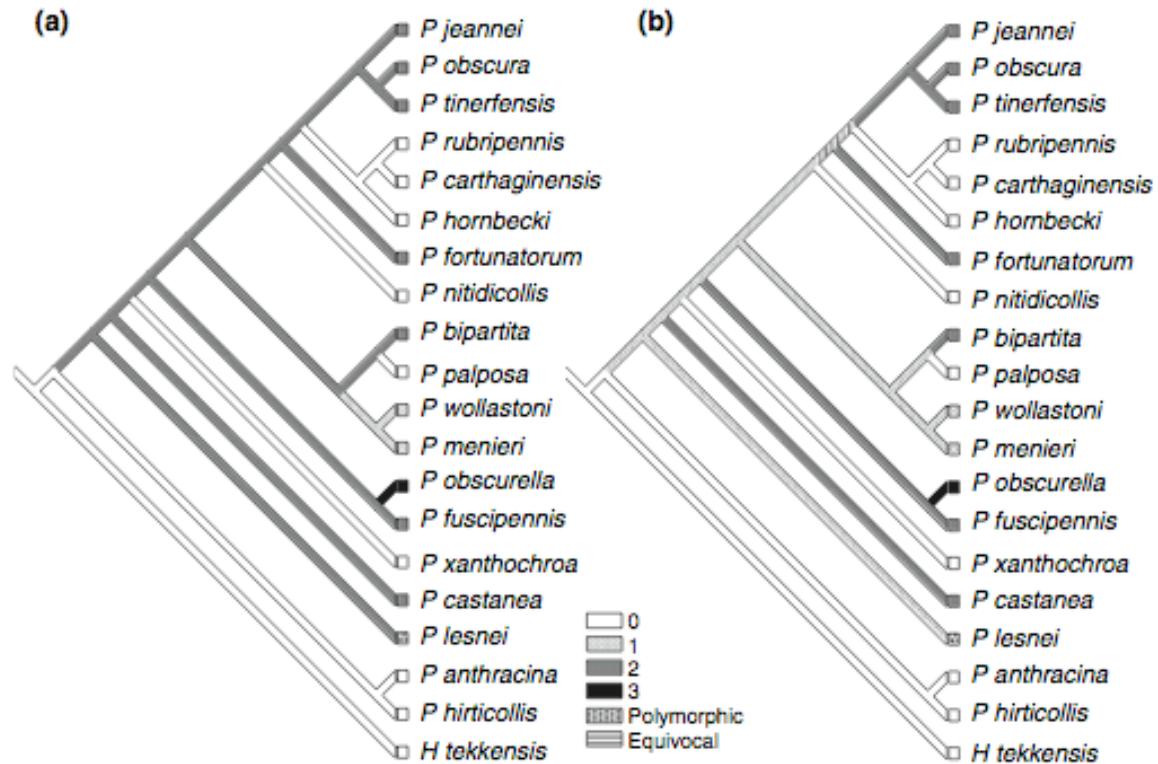
1980s-2000s: diversity of methods in use

Table 2 Historical biogeographic techniques listed under the corresponding approaches and with their original authors. ‘Reconciled trees’ may also be listed under cladistic biogeography

Techniques	Author(s)
Centre of origin and dispersal	Matthew (1915)
Panbiogeography	
Track analysis	Croizat (1958)
Spanning graphs	Page (1987)
Track compatibility	Craw (1988)
Phylogenetic biogeography	Brundin (1966)
Ancestral areas	
Camin & Sokal optimization	Bremer (1992)
Fitch optimization	Ronquist (1994)
Weighted Fitch optimization	Hausdorf (1998)
Cladistic biogeography	
Reduced area cladogram	Rosen (1978)
Ancestral species map	Wiley (1980)
Quantitative phylogenetic biogeography	Mickevich (1981)
Component analysis	Nelson & Platnick (1981)
Brooks parsimony analysis	Wiley (1987)
Component compatibility	Zandee & Roos (1987)
Quantification of component analysis	Humphries <i>et al.</i> (1988)
Three-area statements	Nelson & Ladiges (1991)
Integrative method	Morrone & Crisci (1995)
WISARD	Enghoff (1996)
Paralogy free subtrees	Nelson & Ladiges (1996)
Vicariance events	Hovenkamp (1997)
Event-based methods	
Coevolutionary 2-dimensional cost matrix	Ronquist & Nylin (1990)
Dispersal-vicariance analysis	Ronquist (1997a)
Reconciled trees (Maximum cospeciation)	Page (1994a, b)
Jungles	Charleston (1998)
Combined method	Posadas & Morrone (in press)
Phylogeography	Avise <i>et al.</i> (1987)
Parsimony analysis of endemism	
Localities	Rosen (1988)
Areas of endemisms	Craw (1988)
Quadrats	Morrone (1994)
Experimental biogeography	Haydon <i>et al.</i> (1994)

1980s-2000s: parsimony methods

Figure 1 Parsimony-based optimization of the geographic distribution of the Canary Island species of *Pachydema* (Coleoptera, Scarabaeoidea) and related African species, onto a morphology-based phylogeny (one of three most parsimonious trees, I. Sanmartín, unpublished data); Outgroup: *Hemictenius tekkensis*. (a) Fitch (unordered) optimization; (b) Wagner (ordered) optimization. The Wagner optimization is four steps longer than the Fitch optimization. Area codes: (0) Mainland: Africa/Asia Minor; (1) eastern Canary Islands (Lanzarote and Fuerteventura); (2) central Canary Islands (Gran Canaria, Tenerife, La Gomera); (3) western Canary Islands (La Palma, El Hierro); (polymorphic) widespread in two or more island groups.



Dispersal versus Vicariance

Opinion TRENDS in Ecology and Evolution Vol.20 No.2 February 2005 Full text provided by www.sciencedirect.com SCIENCE @ DIRECT®

The resurrection of oceanic dispersal in historical biogeography

Alan de Queiroz
2695 Mineral Drive, Ely, NV 89301, USA

Geographical distributions of terrestrial or freshwater taxa that are broken up by oceans can be explained by either oceanic dispersal or vicariance in the form of fragmentation of a previously contiguous landmass. The validation of plate-tectonics theory provided a global vicariance explanation, although cladistic arguments for the primacy of vicariance, helped create a view of oceanic dispersal as a rare phenomenon and an explanation of last resort. Here, I describe recent work that suggests that the importance of oceanic dispersal has been strongly underestimated. In particular, molecular dating of lineage divergences favors oceanic dispersal over tectonic vicariance as an explanation for disjunct distributions in a wide variety of taxa, from frogs to beetles to baobab trees. Other evidence, such as substantial gene flow among island populations of *Anolis* lizards, also indicates unexpectedly high frequencies of oceanic dispersal. The resurrection of oceanic dispersal is the most striking aspect of a major shift in historical biogeography toward a more even balance between vicariance and dispersal explanations. This new view implies that biotas are more dynamic and have more recent origins than had been thought previously. A high frequency of dispersal also suggests that a fundamental methodological assumption of many biogeographical studies – that vicariance is *a priori* a more probable explanation than dispersal – needs to be re-evaluated and perhaps discarded.

Glossary

Area cladogram: a cladogram in which the taxa have been replaced by the areas in which they occur. From an area cladogram, various algorithms can be used to derive a maximum likelihood tree in which a single area is associated with each terminal node and each area is represented once. A resolved area cladogram is meant to reflect the history of biotic connections among areas for that group [7]. For example, if areas A and B are grouped together in a resolved area cladogram, it means that the last common ancestor of A and B had a more recent biotic connection to each other than either did to C. Area

"A high frequency of dispersal also suggests that a fundamental methodological assumption of many biogeographical studies -- that vicariance is *a priori* a more probable explanation than dispersal -- needs to be re-evaluated and perhaps discarded."

de Queiroz, A. (2005). "The resurrection of oceanic dispersal in historical biogeography." TREE, 20(2).

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GUEST EDITORIAL



Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands

Robert H. Cowie* and Brenden S. Holland

ABSTRACT

Vicariance biogeography emerged several decades ago from the fusion of cladistics and plate tectonics, and quickly came to dominate historical biogeography. The field has since been largely constrained by the notion that only processes of vicariance and not dispersal offer testable patterns and refutable hypotheses, dispersal being a random process essentially adding only noise to a vicariant system. A consequence of this thinking seems to have been a focus on the biogeography of continents and continental islands, considering the biogeography of oceanic islands less worthy of scientific attention because, being dependent on stochastic dispersal, it was uninteresting. However, the importance of dispersal is increasingly being recognized, and here we stress its fundamental role in the generation of biodiversity on oceanic islands that have been created *in situ*, never connected to larger land masses. Historical dispersal patterns resulting in modern distributions, once considered unknowable, are now being revealed in many plant and animal taxa, in large part through the analysis of polymorphic molecular markers. We emphasize the profound evolutionary insights that oceanic island biogeography has provided, and the fact that, although small in area oceanic islands harbour disproportionately high biodiversity and numbers of endemic taxa. We further stress the importance of continuing research on mechanisms generating oceanic island biodiversity, especially detection of general, non-random patterns of dispersal, and hence the need to acknowledge oceanic dispersal as significant and worthy of research.

Keywords
Biodiversity, dispersal, endemism, historical biogeography, hot spot islands, land snails, oceanic islands, Pacific Ocean.

INTRODUCTION

A consequence of this thinking seems to have been a focus on the biogeography of continents and continental islands.

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"We hope, therefore, that the trend identified by de Queiroz (2005) – the resurrection of oceanic dispersal as important in historical biogeography – is real and that the straightjacket of strict vicariance biogeography is being loosened to include once again the plurality of mechanisms and processes..."

p. 197 of: Cowie, R.H.; Holland, B.S. (2006). "Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands." Journal of Biogeography, 33, 193-198. Emphasis added.

Dispersal versus Vicariance

Journal of Biogeography (J. Biogeogr.) (2007) 34, 1470–1471

CORRESPONDENCE



On basal clades and ancestral areas

During the last 40 years, historical biogeography has been the arena for an apparently endless struggle: the so-called dispersal versus vicariance debate. It is a widespread view that after the 1970s and early 1980s, vicariance dominated historical biogeographical explanations, with dispersal reduced to biogeographical noise wherein no common pattern is able to elucidate the relationships among the areas under inquiry. Most authors see

It is not the aim of the present correspondence to repeat Ebach's (1999) or Morrone's (2002) argumentation against ancestral area analysis, but to reinforce the criticisms already made, adding the points raised by Krell & Cranston (2004) and Crisp & Cook (2005) concerning the relative position of 'more basal' branches in cladograms, which is critical to Bremer's (1992) analytical procedure.

According to Ebach (1999), central to Bremer's ancestral area analysis is Henning's (1966) 'progression rule', which

"During the last 40 years, historical biogeography has been the arena for an apparently endless struggle: the so-called dispersal versus vicariance debate."

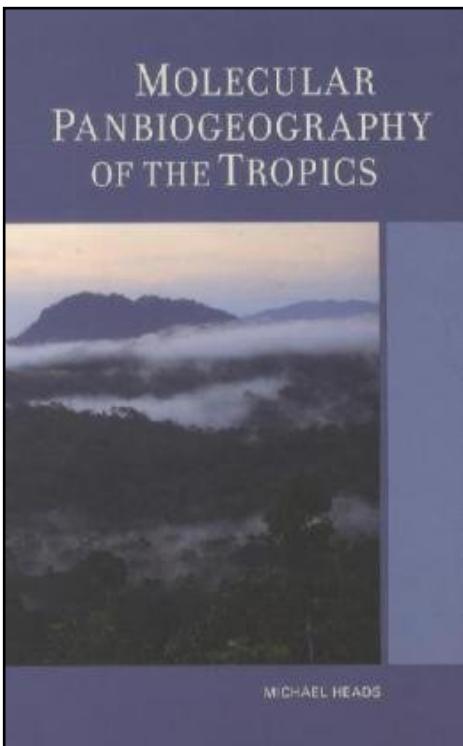
"The resurrection of dispersalism, as de Queiroz (2005) has envisioned, is reactionary and with little (or even no) empirical foundation."

Santos, C.M.D. (2007). "On basal clades and ancestral areas." *Journal of Biogeography*, 34, 1470-1469.

"Most modern biogeographers follow Mayr...in accepting that allopatry can be found by vicariance (dichopatry) or by founder dispersal (peripatry), but only vicariance is accepted here."

"founder dispersal...is controversial and may not exist."

p. 15 in: Heads, M.J. (2012) *Molecular panbiogeography of the tropics*. University of California Press, Berkeley, CA.

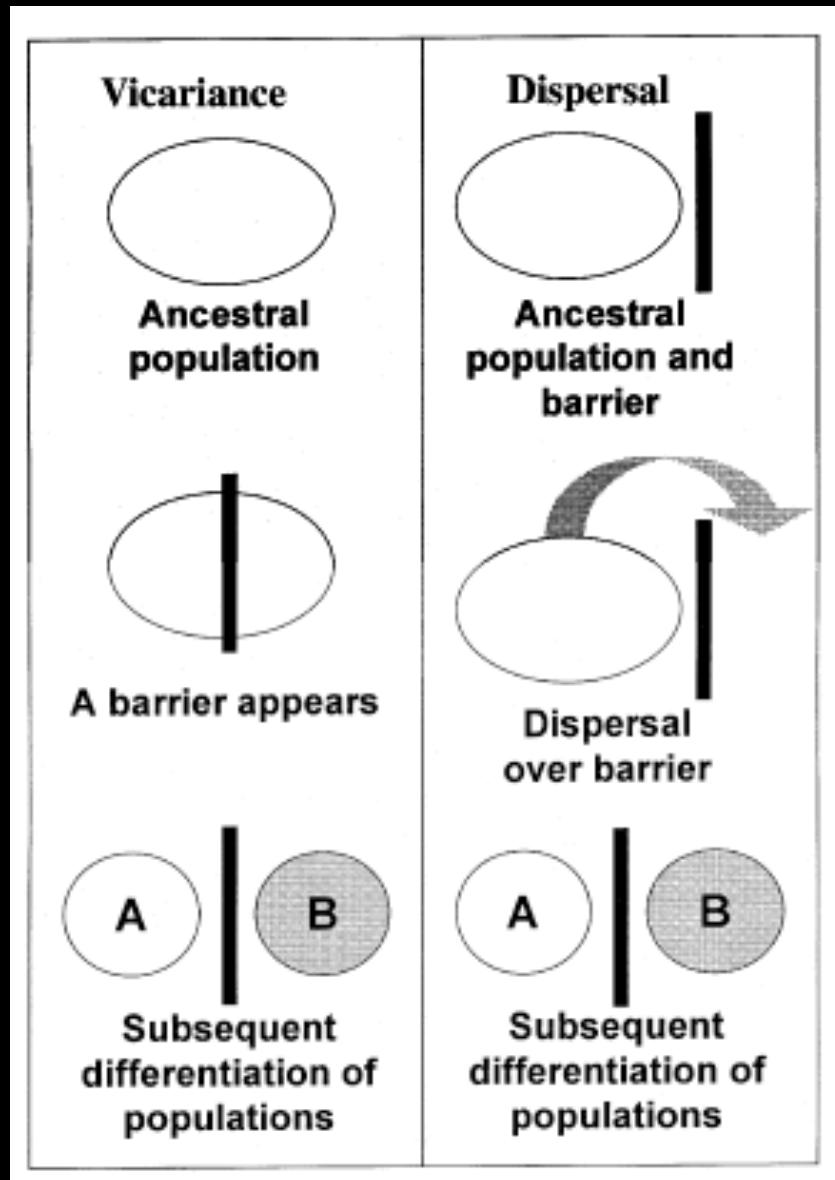


Summary: dispersal versus vicariance

Summary: dispersal versus vicariance

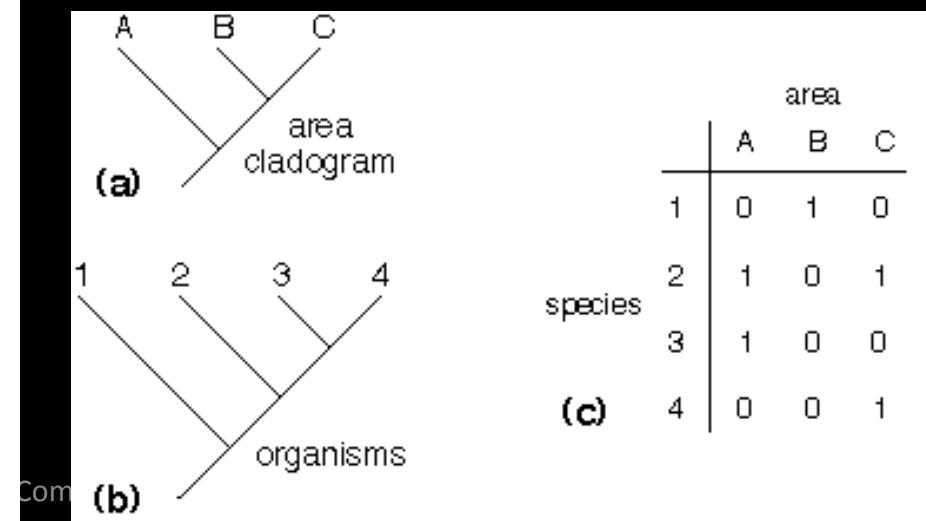


2000s: event-based methods



DIVA -- Dispersal/Vicariance Analysis
-- Ronquist (1997)

- derived from host/parasite cophylogeny etc.
- cost of 1 assigned to dispersal & extinction
- cost of 0 to vicariant speciation

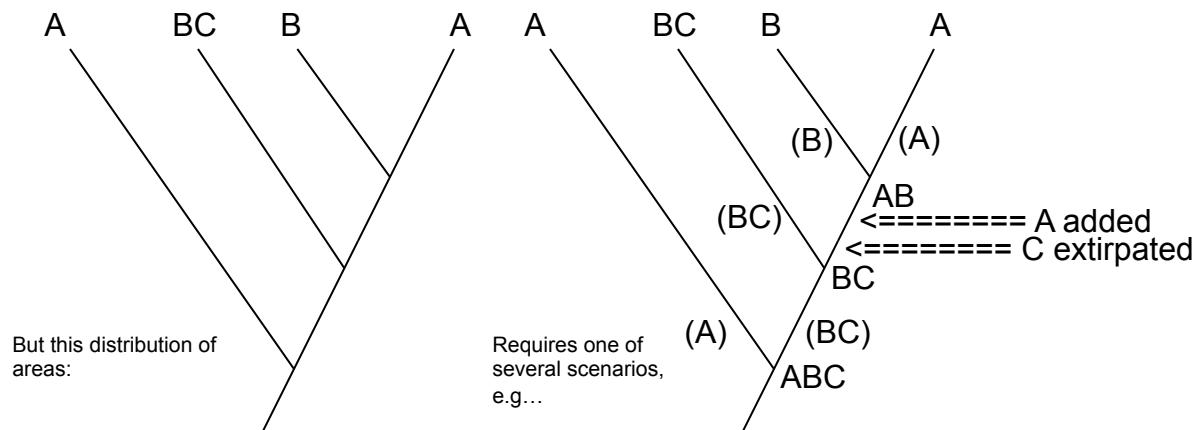
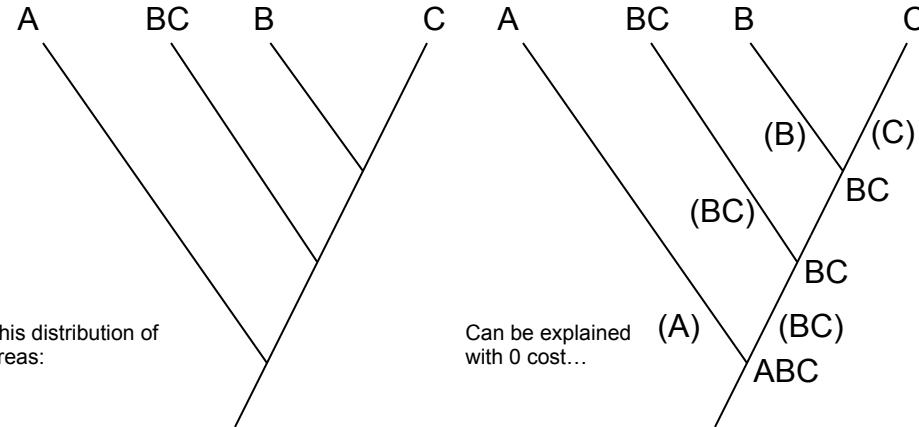


N=number of areas

E.g., if N=3 areas:
Areas = A, B, C

Number of ranges = $2^N - 1$
= 7 possible ranges:

1. Null (excluded)
2. A
3. B
4. C
5. AB
6. AC
7. BC
8. ABC



2005: Maximum Likelihood

Implemented in:
AReA

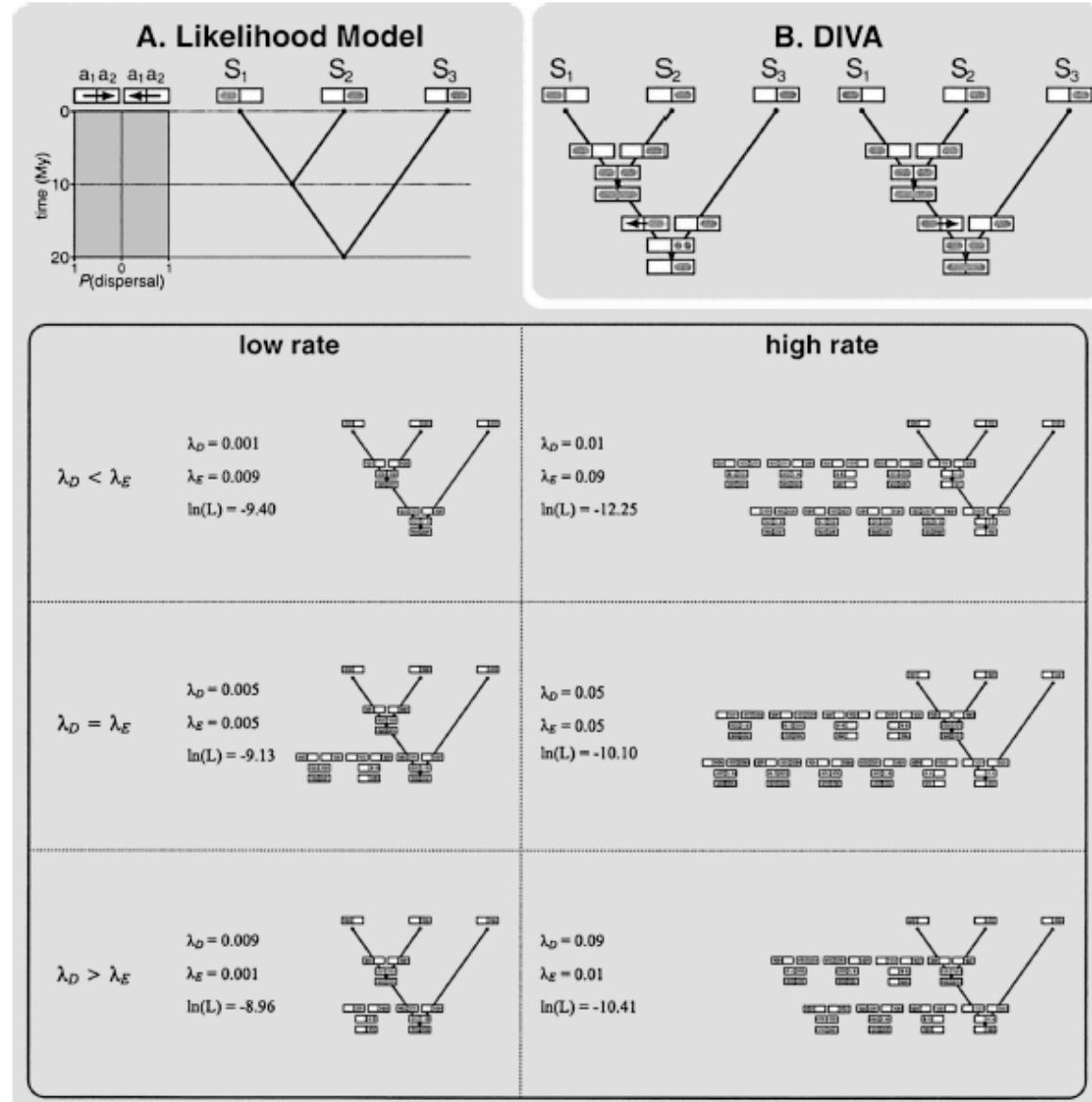


FIG. 4. (A) Likelihood inference of lineage geohistory for a hypothetical three-species phylogeny. The model includes two areas (a_1 and a_2) sharing a single connection, through which the probability of successful dispersal is constant over time and symmetrical with respect to direction. Likelihood estimates of ancestral ranges and subdivision-inheritance scenarios were obtained for different relative dispersal rates ($\lambda_D < \lambda_E$, $\lambda_D = \lambda_E$, and $\lambda_D > \lambda_E = 0.1$) and two overall rates, “low” ($\lambda_D + \lambda_E = 0.01$) and “high” ($\lambda_D + \lambda_E = 0.1$). Adjacent to every internal node are scenarios within two log-likelihood units of the maximum, ordered left to right from lowest to highest likelihood. The highest overall likelihood is obtained at a low rate with $\lambda_D > \lambda_E$. (B) Ancestral ranges and implied speciation scenarios inferred with dispersal-vicariance analysis (DIVA). The two equally most-parsimonious reconstructions correspond to the plausible scenarios inferred from the model parameters yielding the highest likelihood, although in the latter case a widespread ancestor at the root is favored.

2005: Maximum Likelihood

Implemented in:
AReA

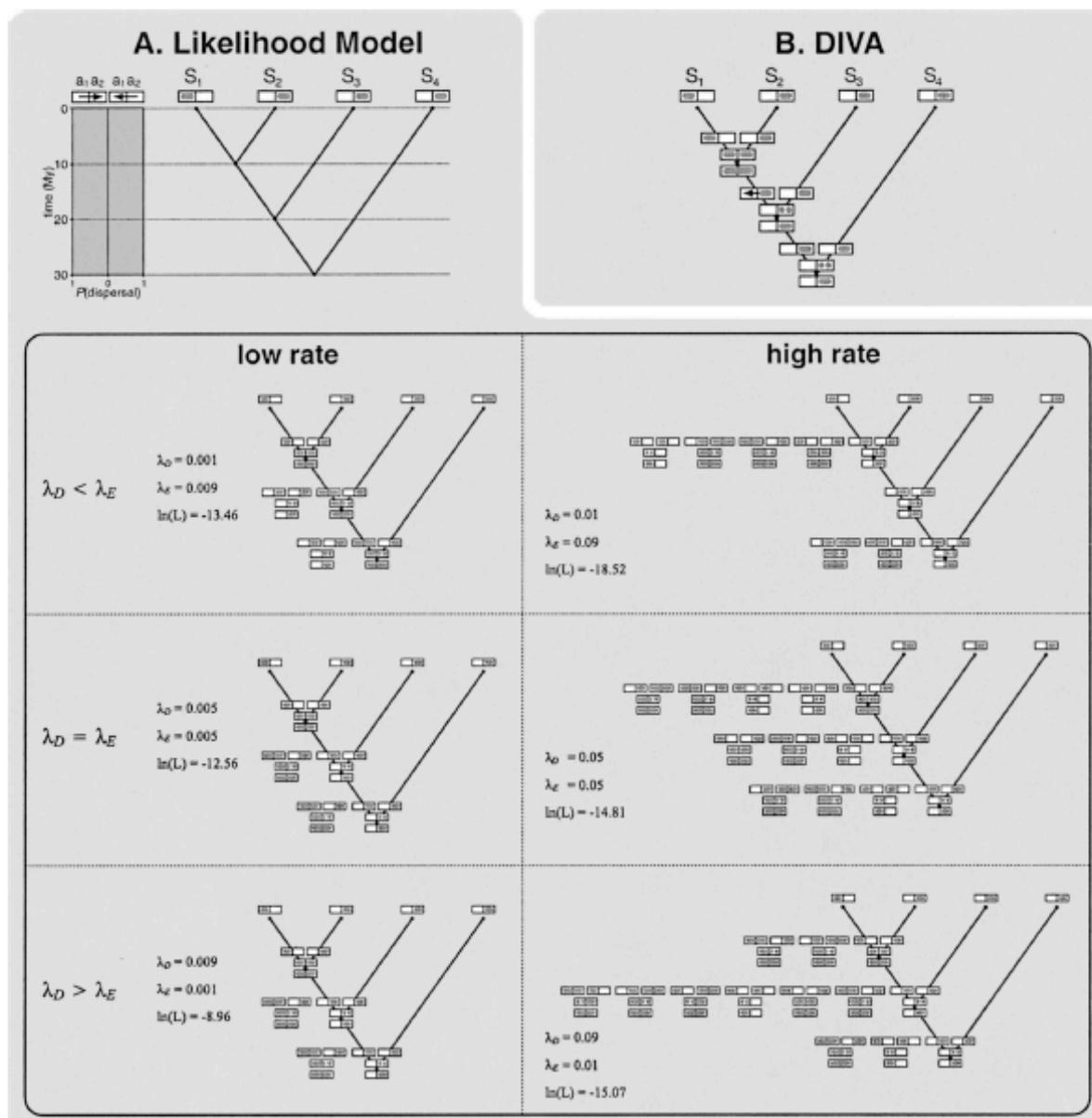


FIG. 5. (A) Likelihood inference of lineage geohistory for a hypothetical four-species example. Components of the geographic model and details of the analyses performed are the same as described previously (Fig. 4A). As in the three-species case, the highest overall likelihood is obtained at a low overall rate with $\lambda_D > \lambda_E$. (B) Ancestral ranges and implied speciation scenarios obtained using dispersal-vicariance analysis (DIVA). The single most-parsimonious reconstruction corresponds to the maximum-likelihood scenarios inferred in (A) but in the latter analysis, alternative scenarios cannot be statistically ruled out.

2008: First Bayesian method

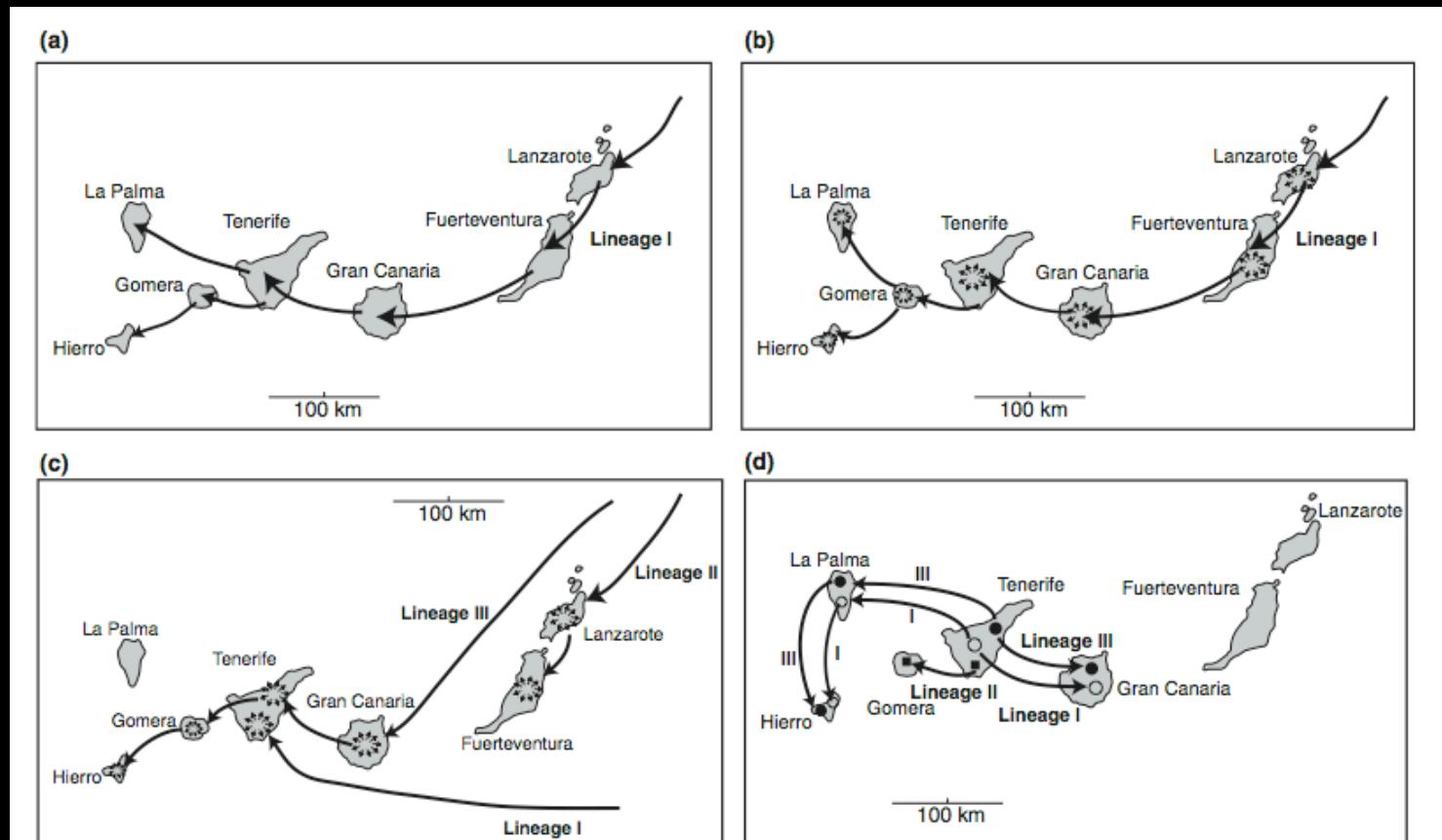


Figure 5 Some common modes of species diversification in Canarian animals and plants. (a) Model I: Stepwise colonization with concomitant speciation resulting in a single species on each island. (b) Model II: Stepwise colonization with speciation followed by within-island speciation; each species has its closest relative in the same island. (c) Model III: Multiple independent colonization events from the mainland (or even back-colonization events of continental areas), followed by within-island speciation. (d) Model IV: Inter-island colonization between similar ecological habitats; each species has its closest relative in a different island but occupying a similar habitat (geometric symbols). The last mode of speciation is common in plants.

2008: First Bayesian method

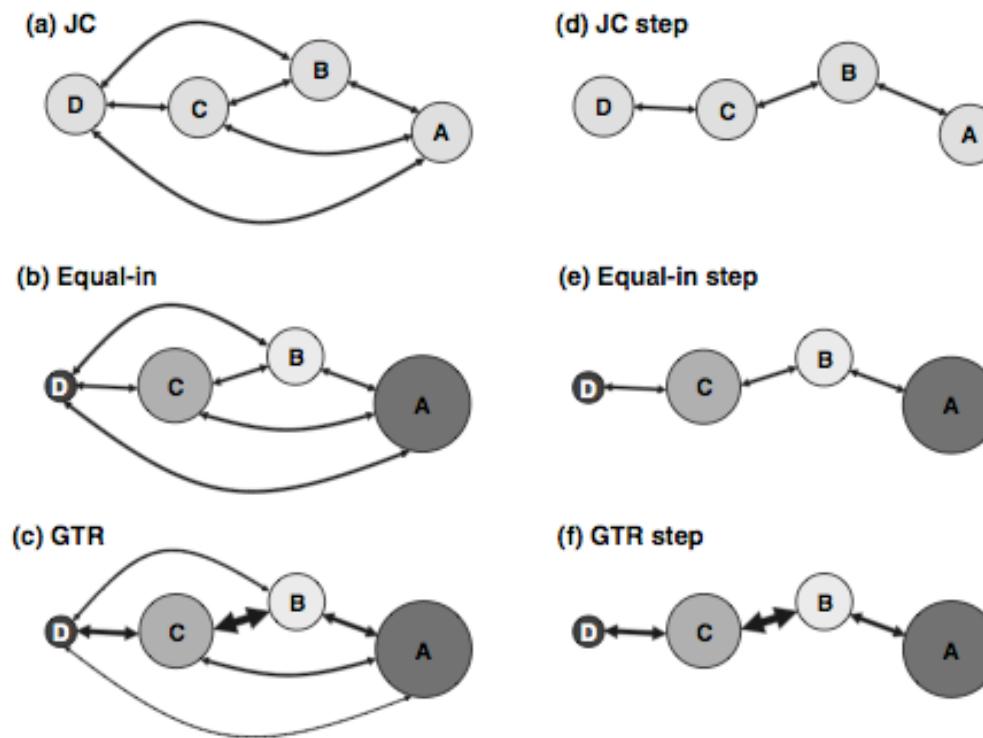


Figure 2 Bayesian Island Models: Each circle represents an island; circle size represents the relative carrying capacity of the island (expected number of lineages at equilibrium); arrow width represents the relative dispersal rate between two single islands. (a) Jukes–Cantor (JC) model: all carrying capacities equal, all dispersal rates equal. (b) Equal-in model: unequal carrying capacities, equal dispersal rates. (c) General Time Reversible (GTR) model: unequal carrying capacities, unequal dispersal rates. (d–f) Stepping-stone variant of each model. (d) JC step: all carrying capacities equal, dispersal rates equal between adjacent islands, zero between non-adjacent islands. (e) Equal-in step: unequal carrying capacities, all dispersal rates equal between adjacent islands, zero between non-adjacent islands. (f) GTR step: all carrying capacities unequal, all dispersal rates unequal between adjacent islands, zero between non-adjacent islands.

2008: First Bayesian method

Table 3 Bayes Factor comparison of different models of island evolution. Models have been ordered according to increasing model likelihood (harmonic mean). A difference larger than five between two model likelihoods indicates ‘very strong support for the model with the highest likelihood’ (Kass & Raftery, 1995).

Island model	Ln model likelihood
JC step	-101704.09
Equal-in	-101667.87
JC	-101649.92
Equal-in step	-101628.31
GTR	-101624.19
GTR step	-101618.94
	*(-101642.9)

*Model likelihood for the ‘long analysis’ (30 million generations, four runs); see text.

Table 4 Bayesian estimates (mean, standard deviation and 95% credibility interval of the posterior probability distribution) of the parameters of the three best biogeographic island models for our data set.

Model	Mean	Standard deviation	95% credibility interval		PSRF
			Lower	Upper	
EQUAL-IN STEP					
π_M	0.656	0.055	0.542	0.751	1.001
π_E	0.021	0.005	0.012	0.034	1.000
π_C	0.249	0.054	0.157	0.361	1.002
π_W	0.074	0.016	0.046	0.110	1.000
GTR					
π_M	0.633	0.096	0.413	0.785	1.006
π_E	0.012	0.006	0.004	0.026	1.006
π_C	0.208	0.041	0.138	0.299	1.001
π_W	0.147	0.076	0.050	0.343	1.006
r_{ME}	<1.0E-6	<1.0E-6	<1.0E-6	<1.0E-6	1.000
r_{MC}	0.026	0.013	0.010	0.058	1.009
r_{MW}	<1.0E-6	<1.0E-6	<1.0E-6	<1.0E-6	1.000
r_{EC}	0.788	0.096	0.562	0.921	1.005
r_{EW}	<1.0E-6	<1.0E-6	<1.0E-6	<1.0E-6	1.000
r_{CW}	0.187	0.093	0.058	0.407	1.004
GTR STEP					
π_M	0.166	0.003	0.034	0.410	1.023
π_E	0.007	0.047	0.003	0.012	1.006
π_C	0.167	0.098	0.094	0.277	1.007
π_W	0.661	0.131	0.418	0.800	1.013
r_{ME}	0.353	0.131	0.147	0.660	1.022
r_{EC}	0.635	0.007	0.328	0.839	1.021
r_{CW}	0.012	0.055	0.004	0.027	1.006

π_i , island carrying capacity; r_{ij} , relative dispersal rate; M, mainland; E, Eastern islands; C, Central islands; W, Western islands; PSRF, Potential scale reduction factor. This parameter is used for convergence diagnostics; a value close to 1.0 indicates a good sampling from the posterior probability distribution of the parameter.

2008: First Bayesian method

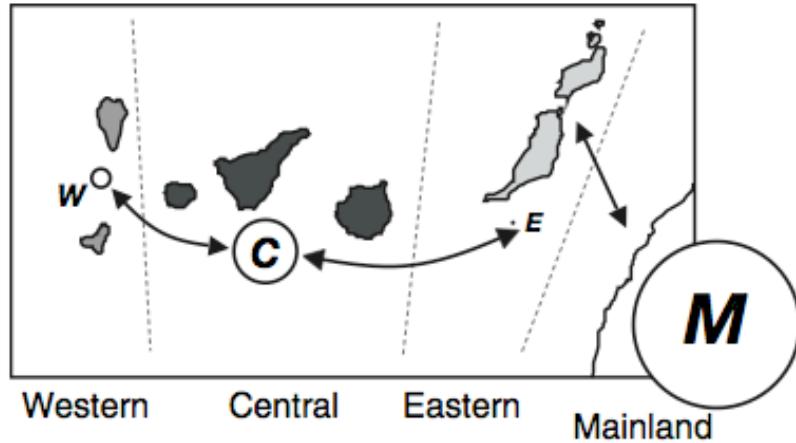


Figure 6 Estimated relative carrying capacities for the Canary Islands based on a data set of 13 Canarian plant and animal phylogenies and using the Equal-in step Bayesian island model. The Canary Islands were divided into three island-groups ('Eastern', Lanzarote and Fuerteventura; 'Central', Gran Canaria, Tenerife and La Gomera; and 'Western', La Palma and El Hierro); 'Mainland' represents non-Canarian distributions (continental areas and Macaronesia). The size of the circles is roughly proportional to the estimated relative carrying capacity for each island-group (see Table 4). The arrow width represents the relative dispersal rate, here 1/3 because the dispersal rate is the same for all island groups and dispersal is only allowed between adjacent island groups ('step model', see Fig. 2e).

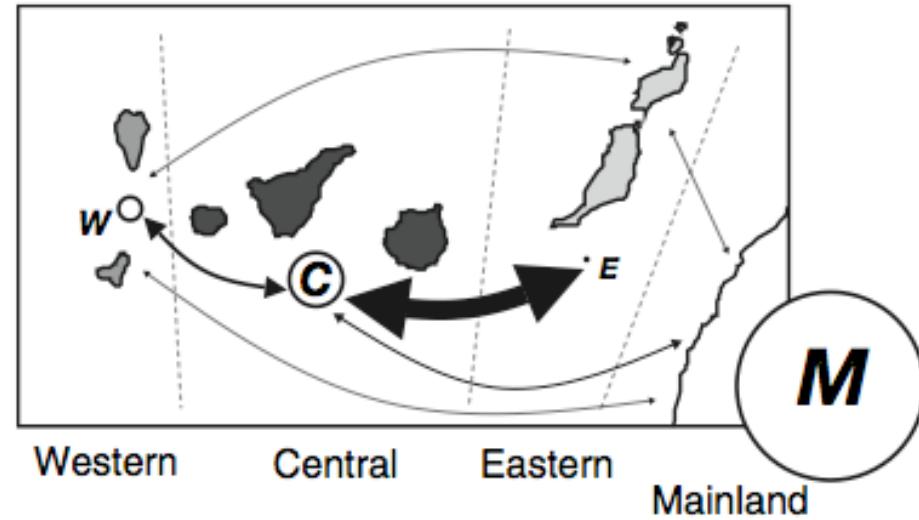


Figure 7 Relative carrying capacities and dispersal rates estimated for the GTR Bayesian island model based on a data set of 13 Canarian plant and animal phylogenies (see Fig. 6 for further explanation).

Critique of available methods

- tend to be “box models”
- how to deal with *multiple* ancestral areas?
- not spatially explicit
- limited number of areas
- sometimes comparative analyses run; few simulation attempts (unlike many other fields)

Pause; then:

Review of assumptions of
main Event-Based Methods

Historical biogeography methods make strong assumptions

- 1. Take a phylogeny**
- 2. Put the geographic ranges at the tips**
- 3. Assume some process(es)**
- 4. Conduct inference
(less important: under parsimony, ML, or Bayesian)**

Main Event-Based Methods

<hr/>					
Software	Statistical method	Max # of areas (under defaults; approximate)	Environmental information?	Phylogenetic information?	Citation count (Google Scholar)
<i>Historical biogeography (inference down a phylogeny):</i>					
Character mapping	parsimony or likelihood	20 discrete areas	no	yes	NA
DIVA (C)	parsimony	12 discrete areas	no	yes	778
Lagrange (Python, C++)	likelihood	12 discrete areas	no	yes	589
BayArea*	Bayesian	almost unlimited	in development	yes	NA

Main Event-Based Methods

Method #1: Treat biogeography as any other discrete character

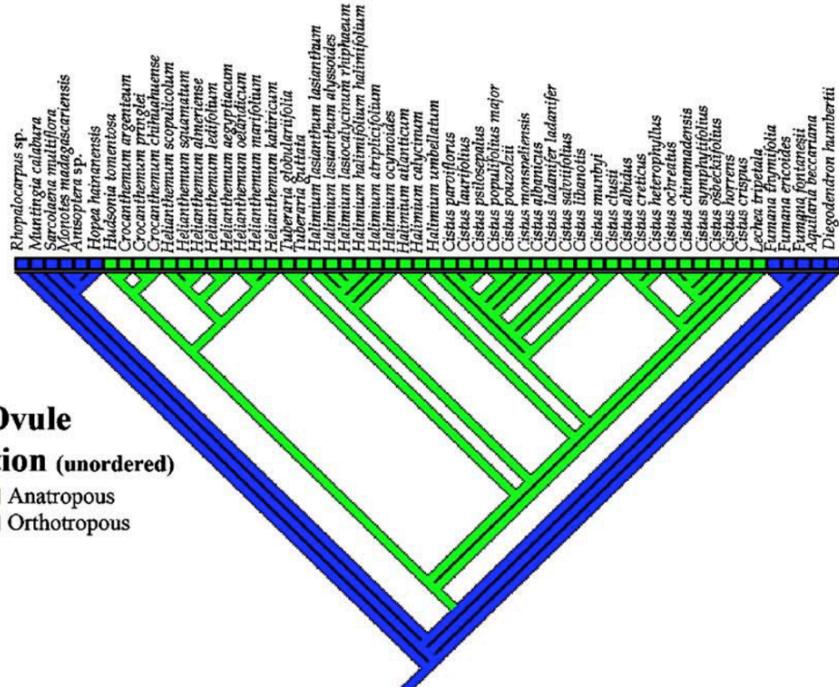
Method #2: DIVA (Dispersal-Vicariance Analysis) -- Ronquist (1997)

Method #3: LAGRANGE (Likelihood Analysis of Geographic Range Evolution)
- Dispersal-Extinction Cladogenesis (DEC)

Method #4: BayArea - Bayesian sampling

Event-based method #1

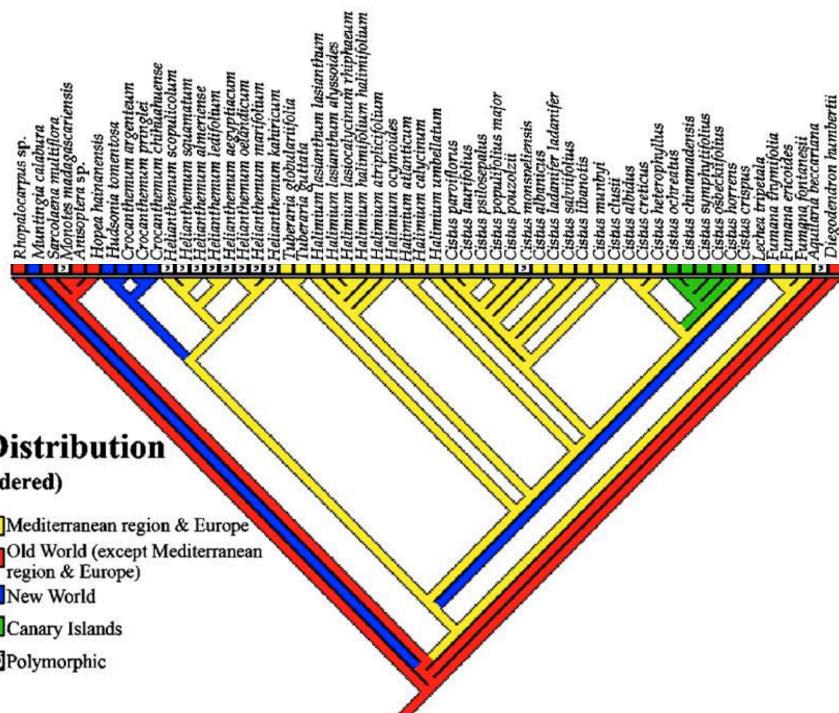
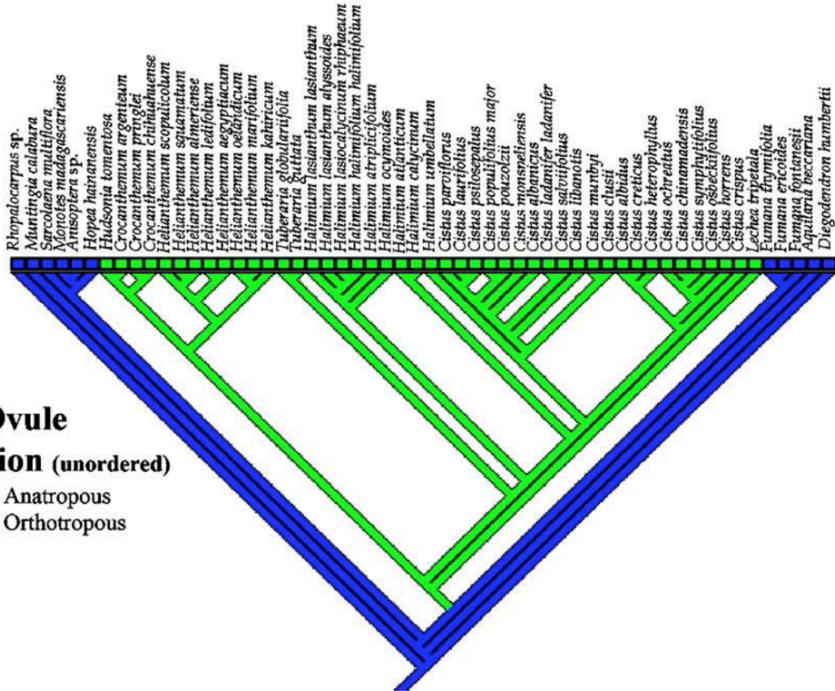
Treat biogeography as any other discrete character



Guzman B, Vargas P (2009). "Historical biogeography and character evolution of Cistaceae (Malvales) based on analysis of plastid rbcL and trnL-trnF sequences." *Organisms, Diversity & Evolution* 9, 83–99.

Event-based method #1

Treat biogeography as any other discrete character



Event-based method #1: Standard character

Assumed model: instantaneous complete range-switching

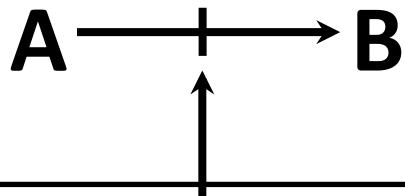
ancestor: descendant:



Event-based method #1: Standard character

Assumed model: instantaneous complete range-switching

ancestor
descendant:

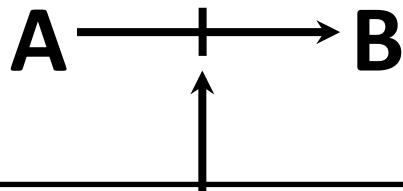


range A suddenly converts to range B

Event-based method #1: Standard character

Assumed model: instantaneous complete range-switching

ancestor → descendant:



range A suddenly converts to range B

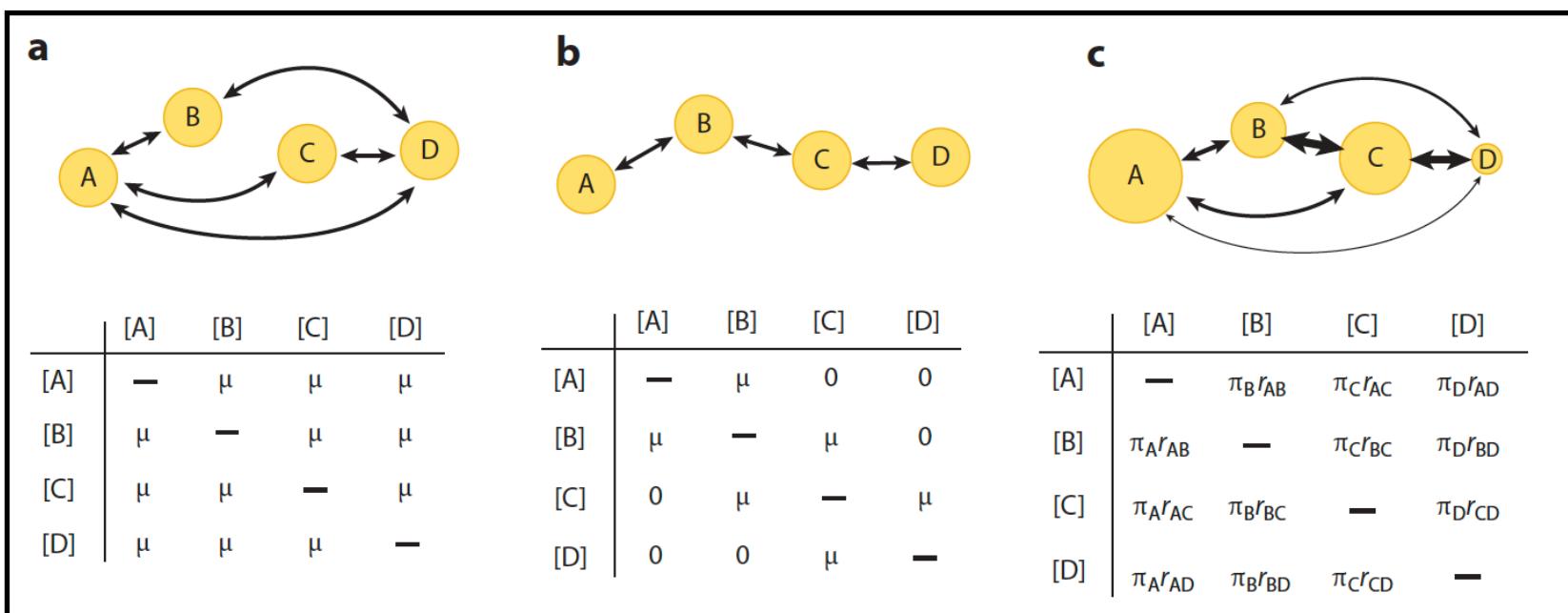
Rate or cost matrix:

	A	B	C	D
A	-	a	a	a
B	a	-	a	a
C	a	a	-	a
D	a	a	a	-

a = rate (or cost) of transition

Event-based method #1: Standard character

Assumed model: instantaneous complete range-switching



Event-based method #2:

DIVA: Dispersal-vicariance analysis (Ronquist 1997)

Lineages are allowed to live in all of the areas

areas: A, B, C

ranges could be: A, B, C, AB, BC, AC, ABC)

Event-based method #2: DIVA: Dispersal-vicariance analysis

Dispersal and extinction events
(along branches) have cost 1:

A => AB (“dispersal” event)
AB => B (“extinction” event)

Event-based method #2: DIVA: Dispersal-vicariance analysis

a	Before	After	Event	DIVA
Anagenetic events			Range expansion (geodispersal)	Yes
			Range contraction (local extinction)	Yes

Event-based method #2: DIVA: Dispersal-vicariance analysis

Vicariance events (at speciation) have cost 0:

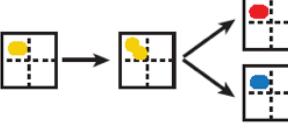
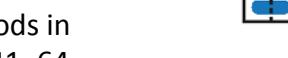
$$AB \Rightarrow A, B$$

Event-based method #2: DIVA: Dispersal-vicariance analysis

a	Before	After	Event	DIVA
Anagenetic events			Range expansion (geodispersal)	Yes
			Range contraction (local extinction)	Yes

Event-based method #2:

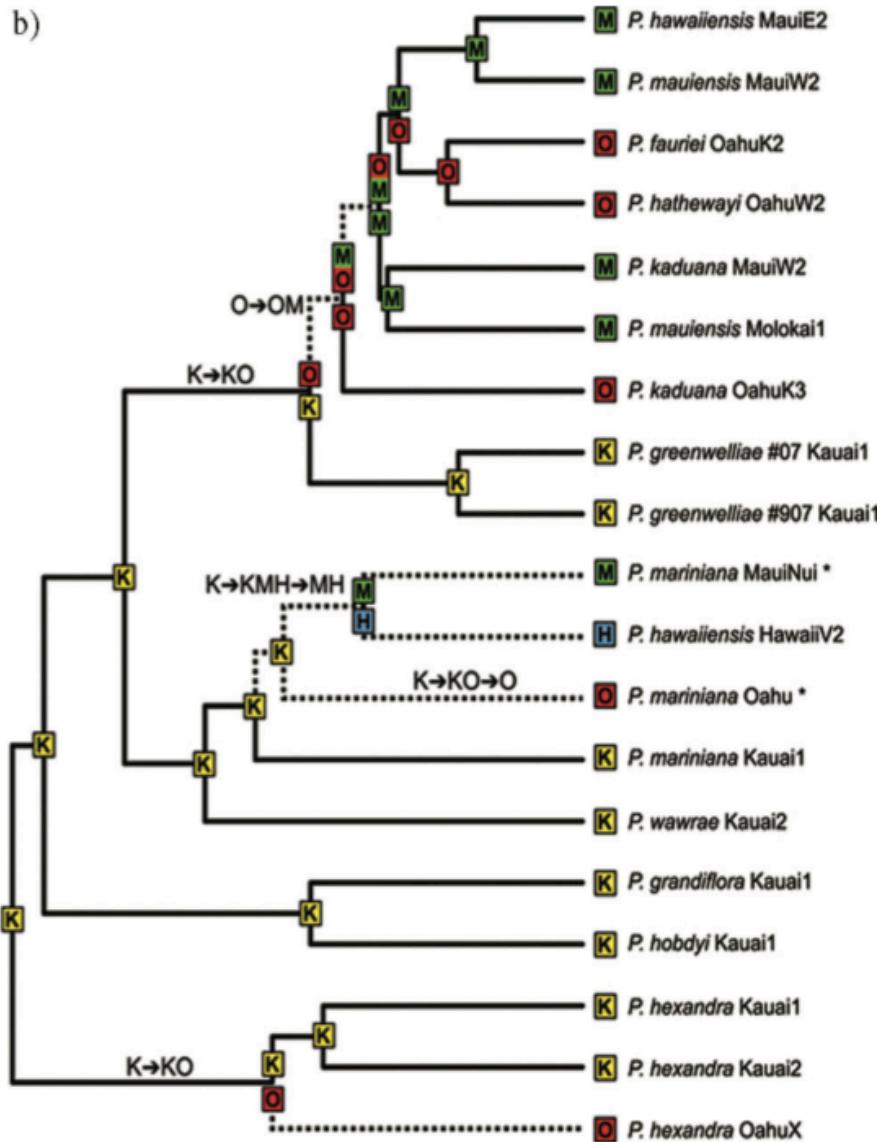
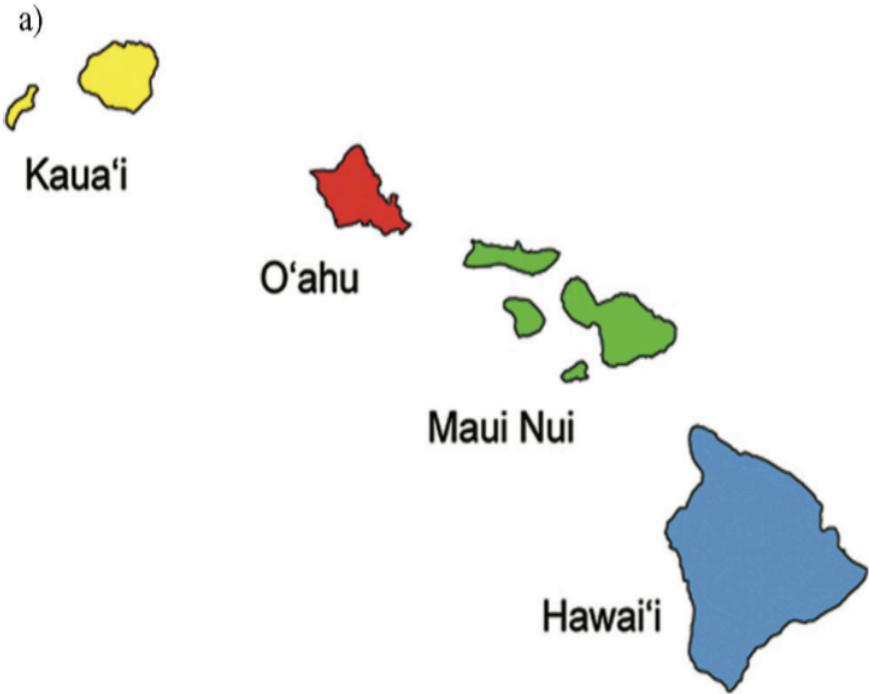
DIVA: Dispersal-vicariance analysis

a	Before	After	Event	DIVA
Anagenetic events			Range expansion (geodispersal)	Yes
			Range contraction (local extinction)	Yes
Cladogenetic events			Duplication (within-area diversification)	Yes
			Sympatric speciation (across multiple areas)	No
			Alloperipatric speciation (one daughter with one area)	Yes
			Peripatric speciation (speciation within one area)	No
			Classical vicariance (both daughters in >1 area)	Yes

Event-based method #3: DEC: Dispersal-extinction cladogenesis

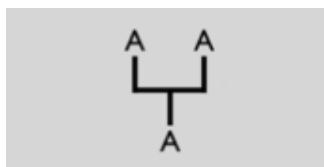
Program: “LAGRANGE”

e.g., Ree & Smith (2008) Hawaiian
Psychotria

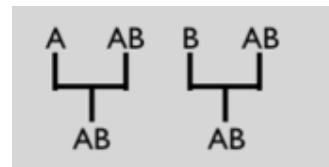


Event-based method #3: DEC: Dispersal-extinction cladogenesis

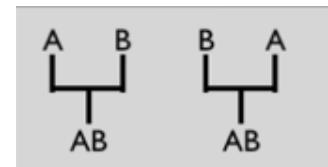
Cladogenesis -- range evolution at speciation events (**LAGRANGE** model)



Weights per speciation event:



subset



vicariance

Event-based method #3:

DEC: Dispersal-extinction cladogenesis

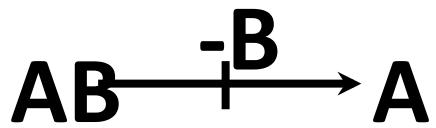
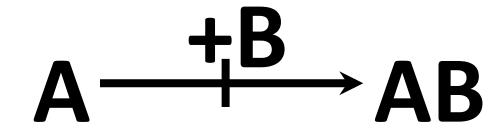
- d = “dispersal” = range extension
- e = “extinction” = range loss
- cladogenesis process

Implemented in the program LAGRANGE

(Likelihood Analysis of Geographic RANGE Evolution)

by Rick Ree & Stephen Smith (2008)

DEC: Dispersal-extinction cladogenesis



“dispersal” event
(really, range expansion)
“extinction” event
(really, extirpation
or
range contraction)

DEC: Dispersal-extinction cladogenesis

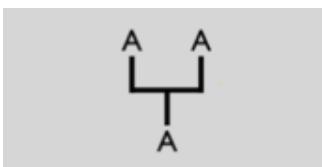
- d = “dispersal” = range extension
- e = “extinction” = range loss

Instantaneous rate matrix:

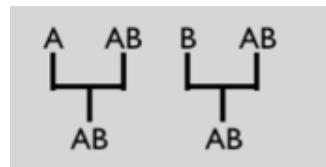
		ending range							
		null	A	B	C	AB	BC	AC	ABC
starting range	null	-	0	0	0	0	0	0	0
	A	e	-	0	0	d	0	d	0
	B	e	0	-	0	d	d	0	0
	C	e	0	-	0	d	d	0	0
	AB	0	e	e	-	0	0	0	$d+d$
	BC	0	0	e	e	-	0	$d+d$	
	AC	0	e	0	e	0	-	$d+d$	
ABC		0	0	0	0	e	e	e	-

DEC: Dispersal-extinction cladogenesis

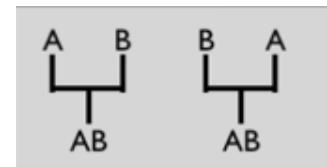
**Cladogenesis -- range evolution at
speciation events**



**Sympatric
speciation
(range
duplication)**



**Sympatric
speciation
(subset)**



**Vicariant
speciation
(range
division)**

Types of speciation, and example descendant ranges:

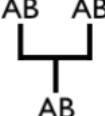
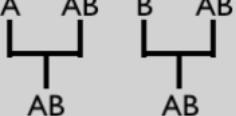
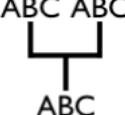
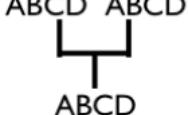
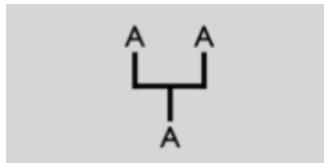
Ancestral ranges:	Sympatric (range copying)	Sympatric (subset)	Vicariance
A		--	--
AB			
ABC			
ABCD			

Figure 1. Various models for the evolution of geographic range at cladogenesis events. The events allowed by LAGRANGE are highlighted in gray. Each allowed event is fixed to have equal probability in the LAGRANGE algorithm.

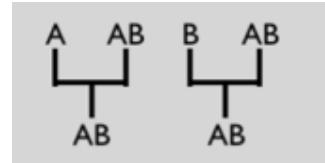
DEC: Dispersal-extinction cladogenesis

Cladogenesis -- range evolution at speciation events (**LAGRANGE** model)

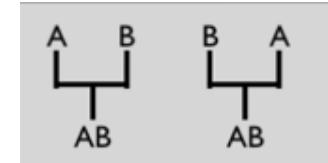
Probabilities per speciation event:



sympatric



subset



vicariance

LAGRANGE: all events equiprobable

Event-based method #2: DIVA: Dispersal-vicariance analysis

a	Before	After	Event	DIVA
Anagenetic events			Range expansion (geodispersal)	Yes
			Range contraction (local extinction)	Yes
Cladogenetic events			Duplication (within-area diversification)	Yes
			Sympatric speciation (across multiple areas)	No
			Alloperipatric speciation (one daughter with one area)	Yes
			Peripatric speciation (speciation within one area)	No
			Classical vicariance (both daughters in >1 area)	Yes

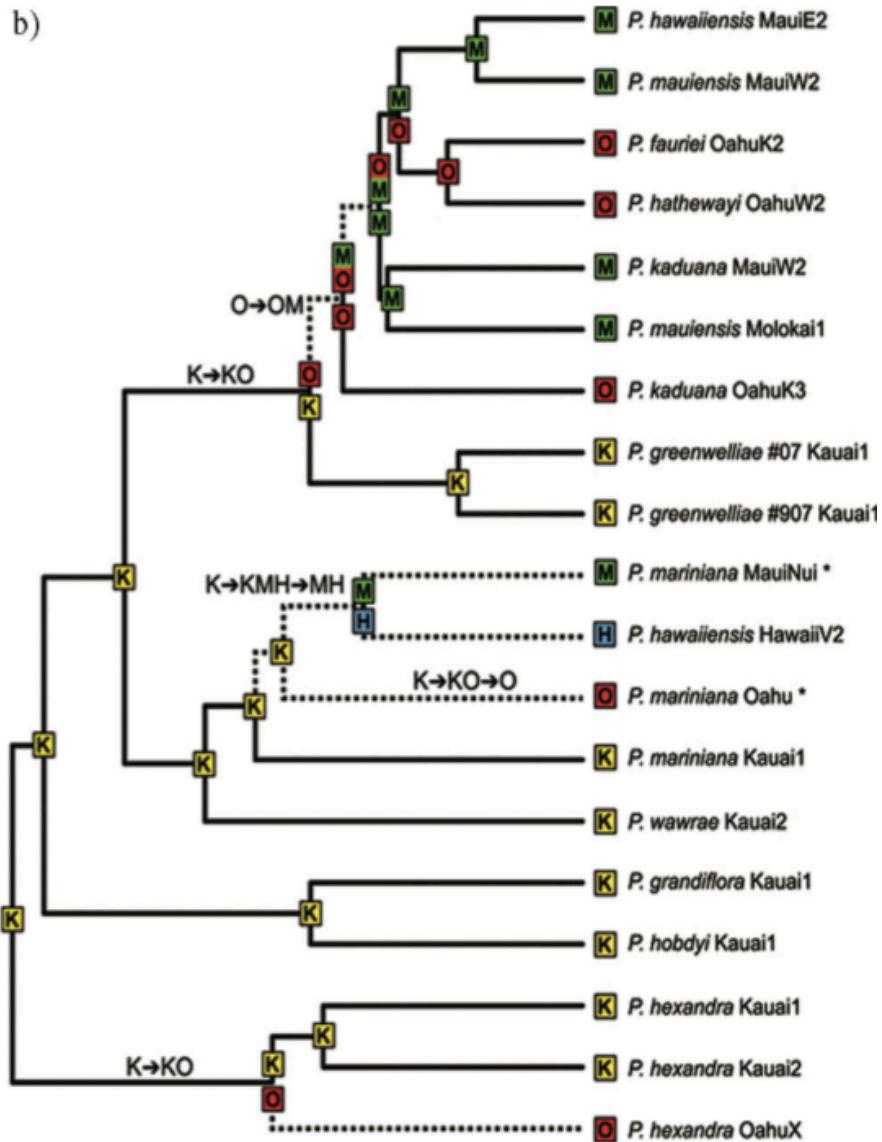
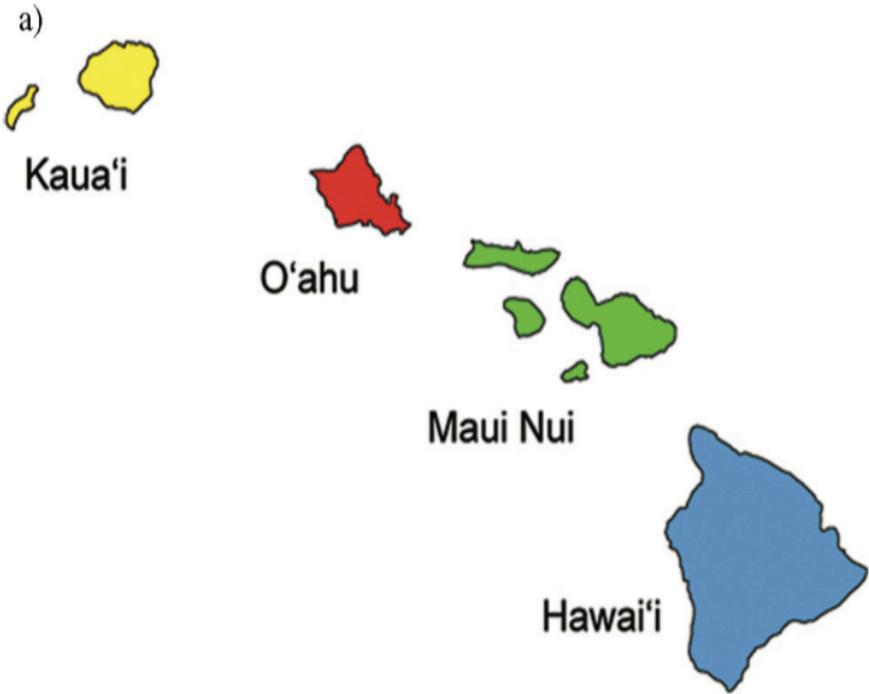
Event-based method #2: DIVA: Dispersal-vicariance analysis

a	Before	After	Event	DIVA	DEC
Anagenetic events			Range expansion (geodispersal)	Yes	Yes
			Range contraction (local extinction)	Yes	Yes
Cladogenetic events			Duplication (within-area diversification)	Yes	Yes
			Sympatric speciation (across multiple areas)	No	No
			Alloperipatric speciation (one daughter with one area)	Yes	Yes
			Peripatric speciation (speciation within one area)	No	Yes
			Classical vicariance (both daughters in >1 area)	Yes	No

Event-based method #3: DEC: Dispersal-extinction cladogenesis

Program: “LAGRANGE”

e.g., Ree & Smith (2008) Hawaiian
Psychotria



Assassin spider biogeography



“State-of-the-art analysis”

Bayes-LAGRANGE

Wood, HM; Matzke, NJ; Gillespie, RG; Griswold, CE (2012). "Treating Fossils as Terminal Taxa in Divergence Time Estimation Reveals Ancient Vicariance Patterns in the Palpimanoidea Spiders." *Systematic Biology*, 62(2), 264-284.

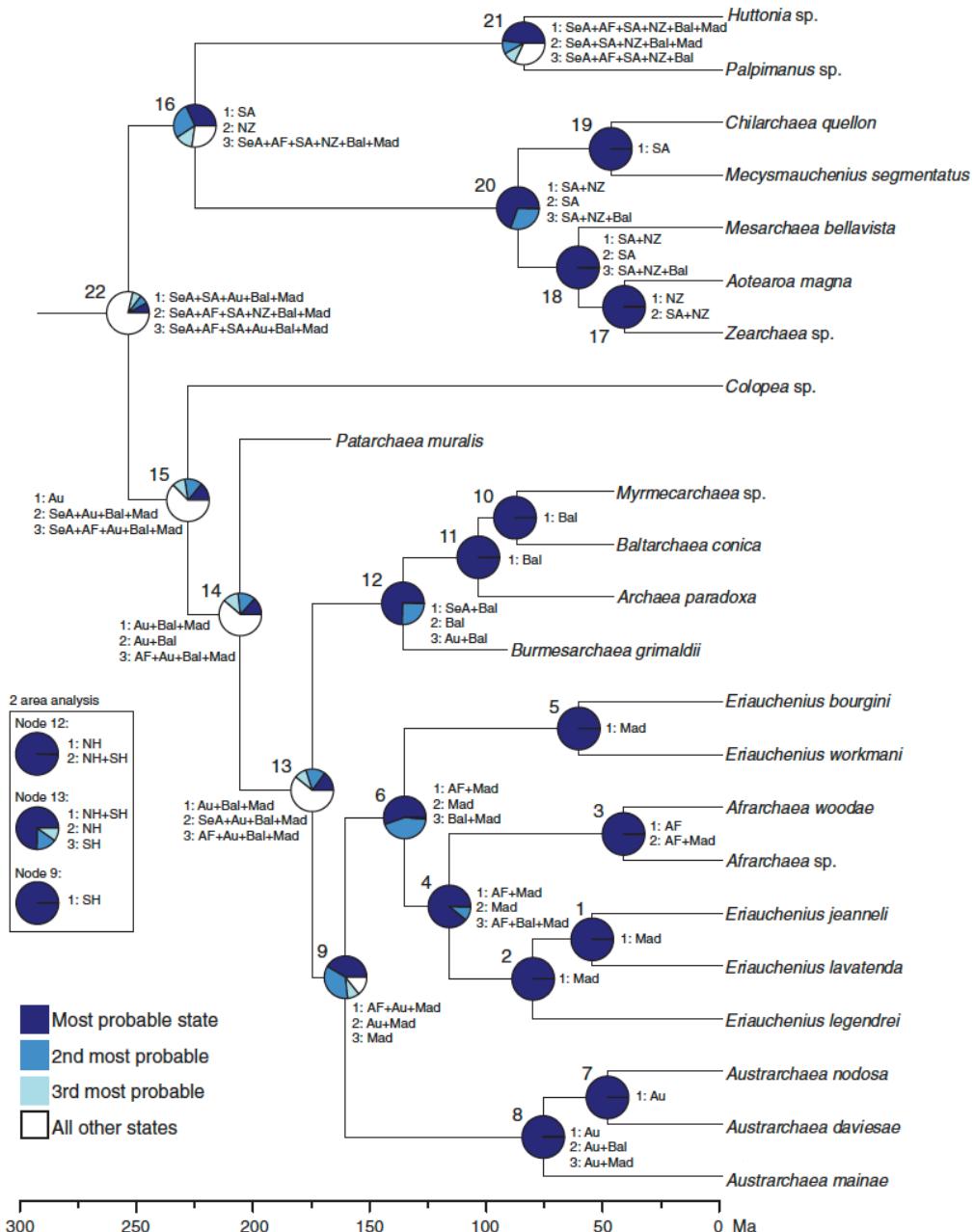


FIGURE 5. Summary of the LAGRANGE ancestral range estimates for the 7-area analysis. LAGRANGE was run on each of 1000 dated phylogenies randomly sampled from the posterior distribution of phylogenies produced during BEAST analysis (v). Pie charts represent the top 3 most likely ancestral geographic ranges at each node. Numbers next to nodes follow Tables 1 and 2. Boxed section summarizes the results from the 2-area analysis for nodes 9, 12, and 13. AF = Africa; Au = Australia; Eu = Eurasia; Mad = Madagascar; NZ = New Zealand; NH = Northern Hemisphere; SA = South America; SeA = Southeast Asia; SH = Southern Hemisphere.

Assassin spider biogeography



“State-of-the-art analysis”

Bayes-DIVA

Wood, HM; Matzke, NJ; Gillespie, RG; Griswold, CE (2012). "Treating Fossils as Terminal Taxa in Divergence Time Estimation Reveals Ancient Vicariance Patterns in the Palpimanoidea Spiders." *Systematic Biology*, 62(2), 264-284.

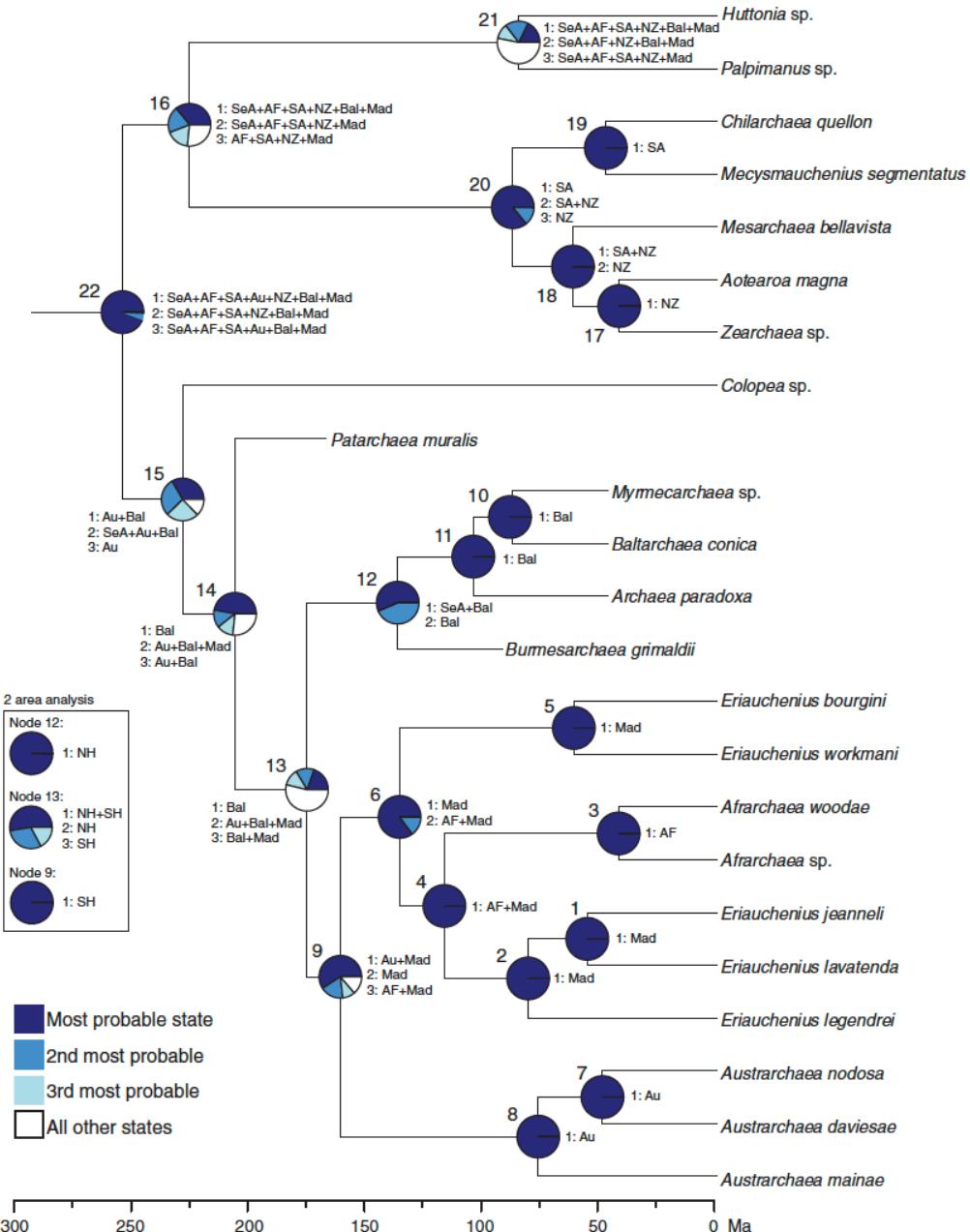


FIGURE 6. Summary of the DIVA ancestral range estimates for the 7-area analysis. DIVA was run on each of 1000 dated phylogenies randomly sampled from the posterior distribution of phylogenies produced during BEAST analysis (v). Pie charts represent the top 3 most likely ancestral geographic ranges at each node. Numbers next to nodes follow Tables 1 and 2. Boxed section summarizes the results from the 2-area analysis for nodes 9, 12, and 13. AF = Africa; Au = Australia; Eu = Eurasia; Mad = Madagascar; NZ = New Zealand; NH = Northern Hemisphere; SA = South America; SeA = Southeast Asia; SH = Southern Hemisphere.

Problems with the state-of-the-art analysis

- Complete range data is assumed
- “true” vicariance is not allowed
 - new species *always* start out at rangesize=1
- Species always start inside their ancestral range
- In LAGRANGE, this cladogenesis model is *fixed and unchangeable*

Bayesian sampling of histories

- Biogeographic rate matrices rapidly get huge ($2^{\text{number of areas}}$)

Statistical Analysis of Biogeography
when the Number of Areas is Large

R.H. Statistical Analysis of Biogeography

MICHAEL J. LANDIS¹, NICHOLAS J. MATZKE¹, BRIAN R. MOORE², AND JOHN P.
HUELSENBECK^{1,3}

¹*Department of Integrative Biology
University of California, Berkeley, CA 94720-3140, U.S.A.*

²*Department of Evolution and Ecology, University of California, Davis
Storer Hall, One Shields Avenue, Davis, CA 95616, U.S.A.*

³*King Abdulaziz University, Jeddah, Saudi Arabia*

See “BayArea” program:
<http://code.google.com/p/bayarea>

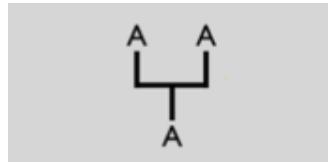
Accepted,
Systematic Biology

Can do hundreds of areas through
Bayesian data augmentation

But, assumes ranges are copied at
cladogenesis

“BayArea” program (Landis et al. 2013)

Cladogenesis -- “no event” during speciation (i.e., pure continuous time)

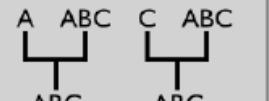
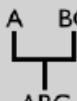
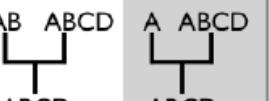
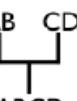
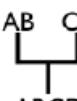


**“Sympatric” (range-copying)
speciation occurs with probability=1.0**

Weights per speciation event:

Different cladogenesis models!

DEC cladogenesis model

	Sympatric (range copying)	Sympatric (subset)	Vicariance
A		--	--
AB		 	 
ABC		 	 
ABCD		 	 

Different cladogenesis models!

DEC cladogenesis model

	Sympatric (range copying)	Sympatric (subset)	Vicariance
Ancestral range	A A A	--	--
	AB AB AB	A AB AB B AB AB	A B AB B A AB
	ABC ABC ABC	A ABC ABC C ABC ABC	A BC ABC B AC ABC
	ABCD ABCD ABCD	AB ABCD ABCD A ABCD ABCD	AB CD ABCD A BCD ABCD

DIVA cladogenesis model

	Sympatric (range copying)	Sympatric (subset)	Vicariance
Ancestral range	A A A	--	--
	AB AB AB	A AB AB B AB AB	A B AB B A AB
	ABC ABC ABC	A ABC ABC C ABC ABC	A BC ABC B AC ABC
	ABCD ABCD ABCD	AB ABCD ABCD A ABCD ABCD	AB CD ABCD A BCD ABCD

BAYAREA cladogenesis model

	Sympatric (range copying)	Sympatric (subset)	Vicariance
Ancestral range	A A A	--	--
	AB AB AB	A AB AB B AB AB	A B AB B A AB
	ABC ABC ABC	A ABC ABC C ABC ABC	A BC ABC B AC ABC
	ABCD ABCD ABCD	AB ABCD ABCD A ABCD ABCD	AB CD ABCD A BCD ABCD

Figure 1. The types of cladogenesis events allowed (gray) and disallowed (white) under the DEC, DIVA, and BAYAREA cladogenesis models. The “+J” version of each model adds founder-event speciation, as illustrated for DEC+J.

Unresolved fundamental issues

What is the right model?

- “Vicariance vs. dispersal”
- Range extension / contraction
- Cladogenic vs. anagenic change
- Founder-event speciation

Unresolved fundamental issues

What is the right model?

- “Vicariance vs. dispersal”
- Range extension / contraction
- Cladogenic vs. anagenic change
- **Founder-event speciation**

Founder-event speciation

- In founder-event speciation, a rare dispersal event “instantaneously” establishes a geographically isolated new lineage with one or a few individuals
- Widely discussed in population genetics, speciation literature, island biogeography
- However, was ignored in historical biogeography computational inference *models*

Types of speciation, and example descendant ranges:

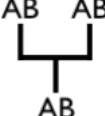
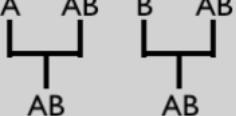
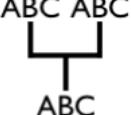
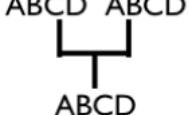
Ancestral ranges:	Sympatric (range copying)	Sympatric (subset)	Vicariance
A		--	--
AB			
ABC			
ABCD			

Figure 1. Various models for the evolution of geographic range at cladogenesis events. The events allowed by LAGRANGE are highlighted in gray. Each allowed event is fixed to have equal probability in the LAGRANGE algorithm.

(remember?) Dispersal versus Vicariance

Journal of Biogeography (*J. Biogeogr.*) (2007) 34, 1470–1471

CORRESPONDENCE



On basal clades and ancestral areas

During the last 40 years, historical biogeography has been the arena for an apparently endless struggle: the so-called dispersal versus vicariance debate. It is a widespread view that after the 1970s and early 1980s, vicariance dominated historical biogeographical explanations, with dispersal reduced to biogeographical noise wherein no common pattern is able to elucidate the relationships among the areas under inquiry. Most authors see

It is not the aim of the present correspondence to repeat Ebach's (1999) or Morrone's (2002) argumentation against ancestral area analysis, but to reinforce the criticisms already made, adding the points raised by Krell & Cranston (2004) and Crisp & Cook (2005) concerning the relative position of 'more basal' branches in cladograms, which is critical to Bremer's (1992) analytical procedure.

According to Ebach (1999), central to Bremer's ancestral area analysis is Henning's (1966) 'progression rule', which

"During the last 40 years, historical biogeography has been the arena for an apparently endless struggle: the so-called dispersal versus vicariance debate."

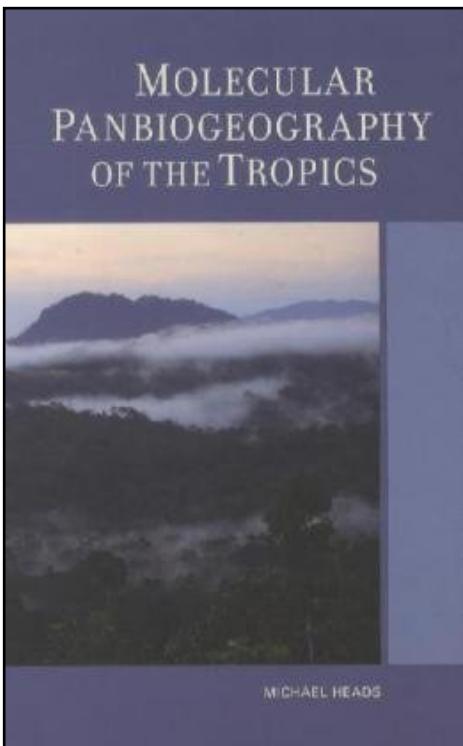
"The resurrection of dispersalism, as de Queiroz (2005) has envisioned, is reactionary and with little (or even no) empirical foundation."

Santos, C.M.D. (2007). "On basal clades and ancestral areas." *Journal of Biogeography*, 34, 1470-1469.

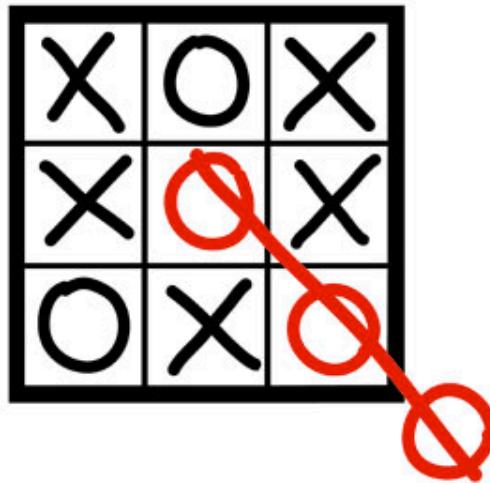
"Most modern biogeographers follow Mayr...in accepting that allopatry can be found by vicariance (dichopatry) or by founder dispersal (peripatry), but only vicariance is accepted here."

"founder dispersal...is controversial and may not exist."

p. 15 in: Heads, M.J. (2012) *Molecular panbiogeography of the tropics*. University of California Press, Berkeley, CA.



**THINK
OUTSIDE
THE BOX**



Types of speciation, and example descendant ranges:

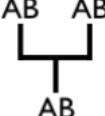
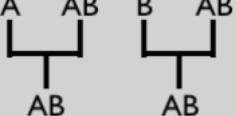
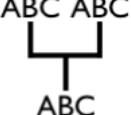
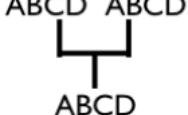
Ancestral ranges:	Sympatric (range copying)	Sympatric (subset)	Vicariance
A		--	--
AB			
ABC			
ABCD			

Figure 1. Various models for the evolution of geographic range at cladogenesis events. The events allowed by LAGRANGE are highlighted in gray. Each allowed event is fixed to have equal probability in the LAGRANGE algorithm.

Types of speciation, and example descendant ranges:

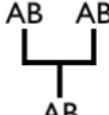
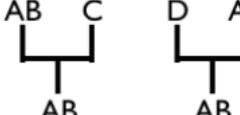
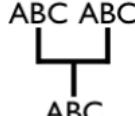
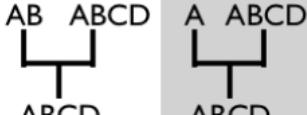
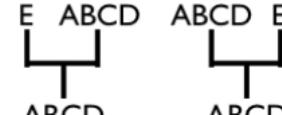
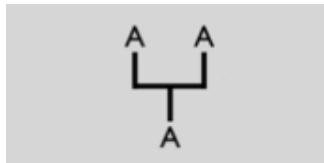
Ancestral ranges:	Sympatric (range copying)	Sympatric (subset)	Vicariance	Founder Event
A		--	--	
AB				
ABC				
ABCD				

Figure 1. Various models for the evolution of geographic range at cladogenesis events. The events allowed by LAGRANGE are highlighted in gray. Each allowed event is fixed to have equal probability in the LAGRANGE algorithm.

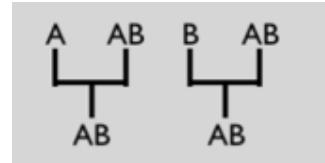
DEC: Dispersal-extinction cladogenesis

Cladogenesis -- range evolution at speciation events (**LAGRANGE** model)

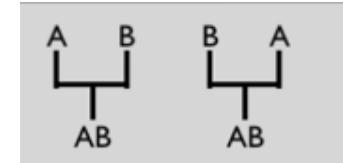
Probabilities per speciation event:



sympatric



subset

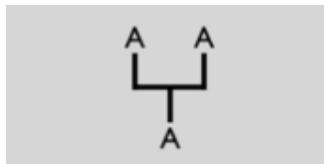


vicariance

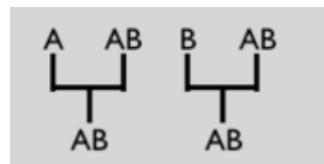
LAGRANGE: all events equiprobable

DECj: Dispersal-extinction cladogenesis PLUS founder- event speciation

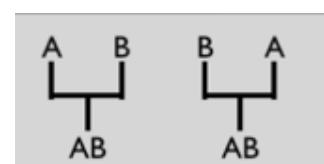
Probabilities per speciation event:



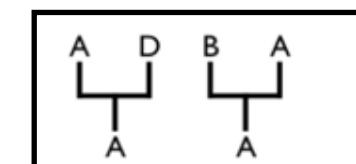
sympatric



subset



vicariance

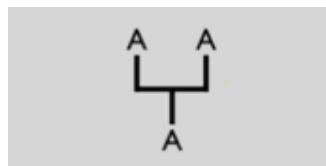


Founder Event

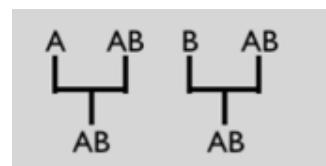
LAGRANGE: all events equiprobable

DECj: Dispersal-extinction cladogenesis PLUS founder- event speciation

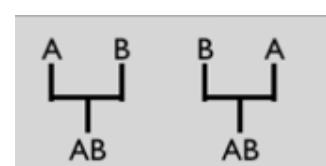
Probabilities per speciation event:



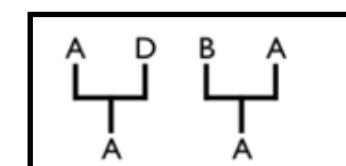
sympatric



subset



vicariance



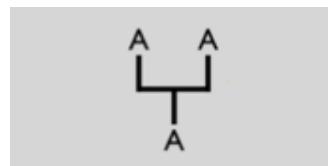
Founder Event

	ending range																						
left:	A	A	A	A	A	A	B	B	B	B	B	C	C	C	C	C	C	C	C	C	C	count	
right:	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	AC	
A	sym	j	j																			1	
B		j	j	sym	j	j																1	
C		j	j		sym	j	j															1	
AB	vic	sub		vic		sub		vic		sub		sub		sub		j	sub	sub	j			6	
BC		vic			vic	sub			vic													6	
AC	vic	sub				vic	sub		vic													6	
ABC	vic	sub					vic	sub		vic												12	

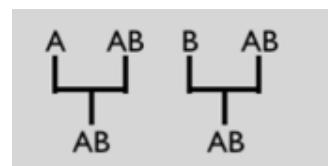
The probability of different events:
controlled by value of parameter j

DECj: Dispersal-extinction cladogenesis PLUS founder- event speciation

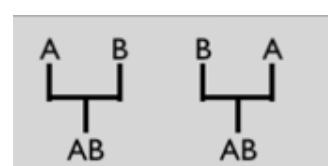
Probabilities per speciation event:



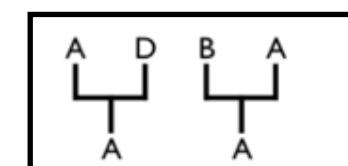
sympatric



subset



vicariance



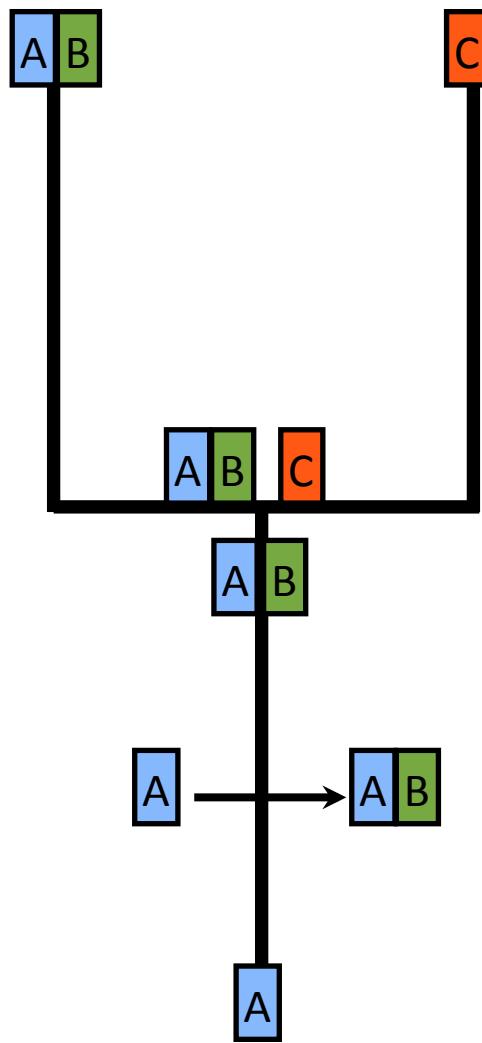
Founder Event

	ending range																								count		
left:	A	A	A	A	A	A	B	B	B	B	B	C	C	C	C	C	C	C	C	C	C	C	C	C	C	count	
right:	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	count	
A	sym		j	j						j					j												count
B			j	j						j					j												count
C																											count
starting range	AB	vic	sub																								count
AB																											count
BC																											count
AC																											count
ABC																											count

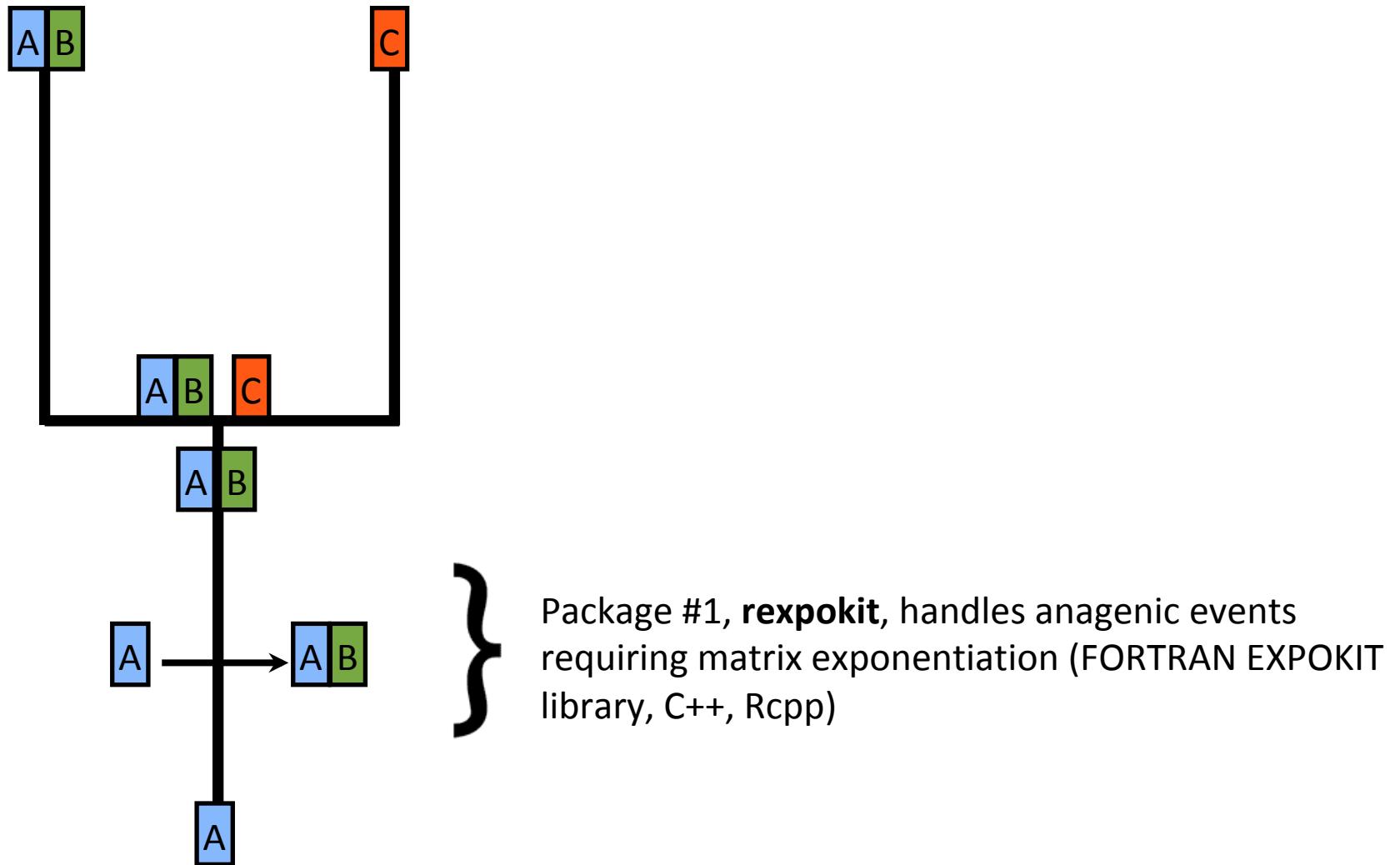
The probability of different events:
controlled by value of parameter j

I implemented this method in *three* R packages:

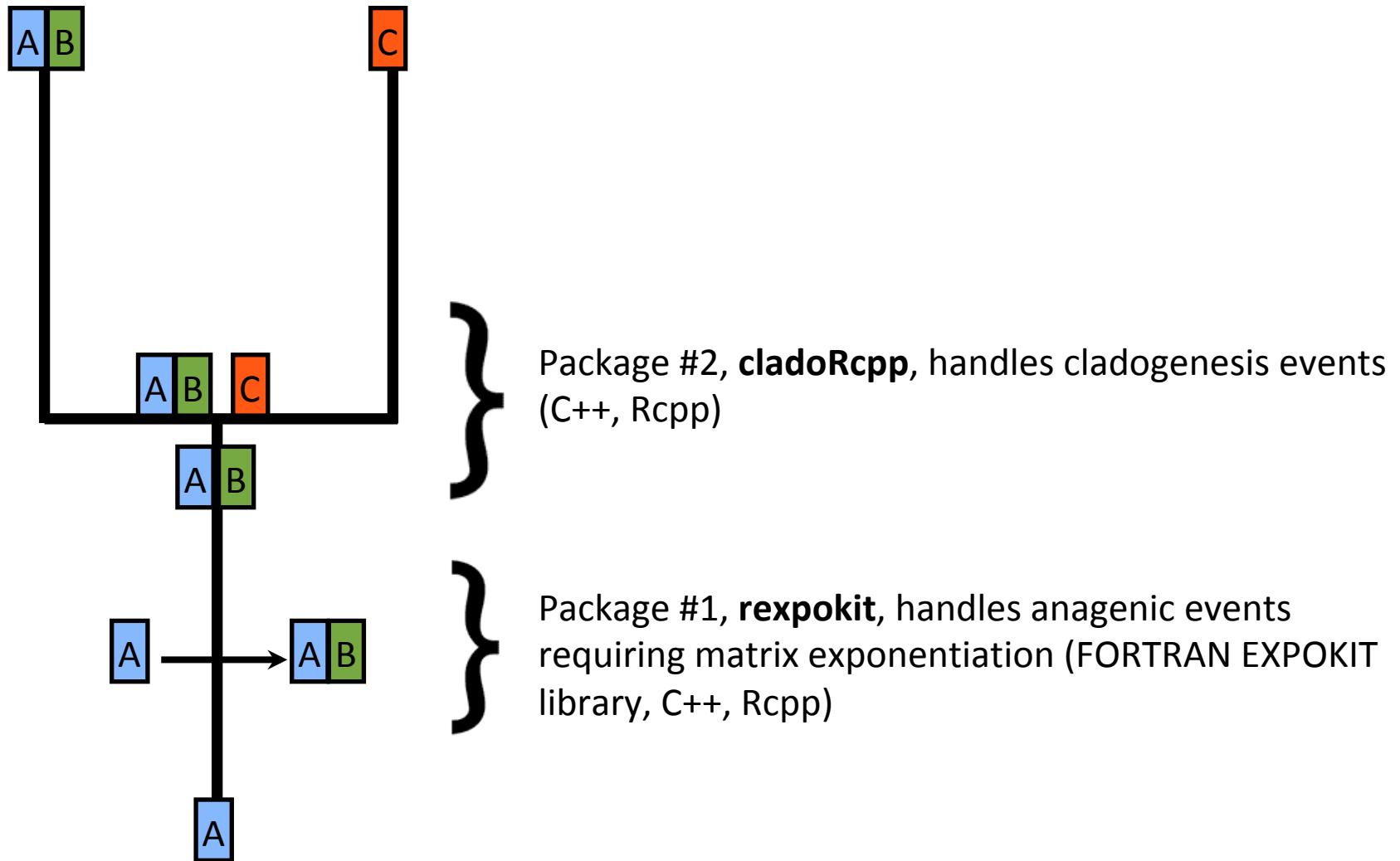
I implemented this method in *three* R packages:



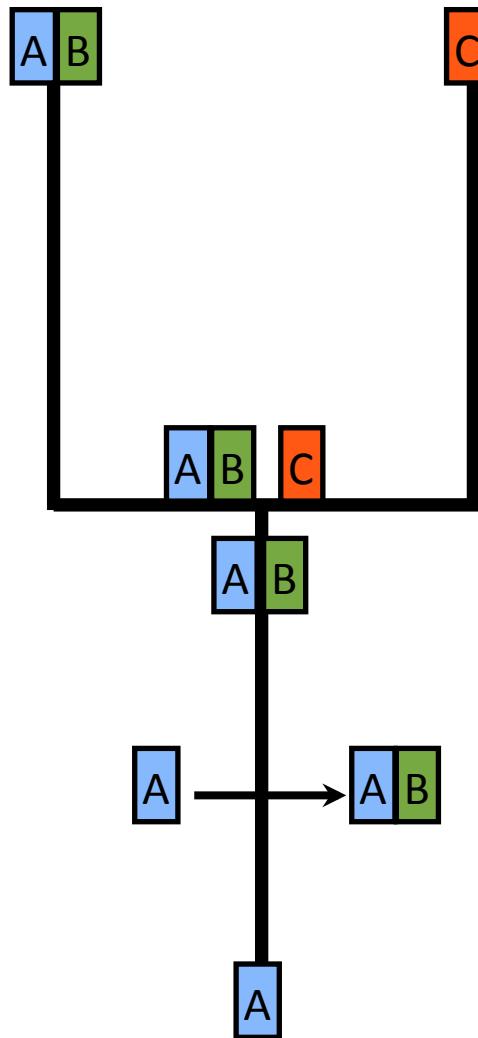
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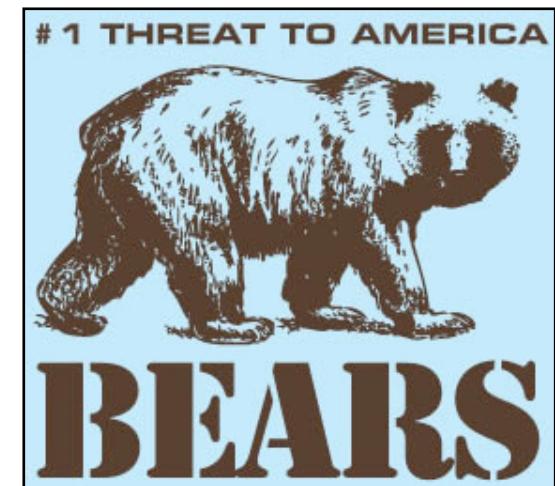


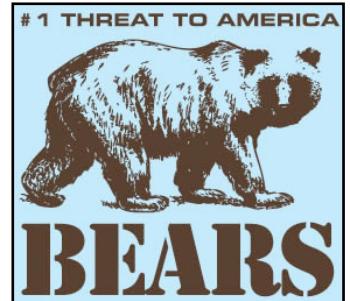
I implemented this method in *three* R packages:



Package #3, **BioGeoBEARS**, does the ML/Bayesian searches, model testing, etc.

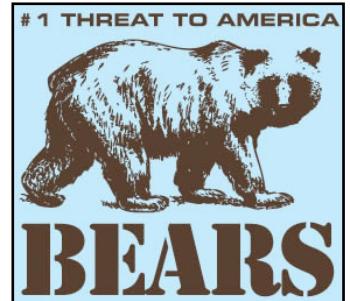
BioGeographic Bayesian Evolutionary Analysis with R Scripts





Like in LAGRANGE, BioGeoBEARS users can load:

- Time strata
- Dispersal multipliers
- Connectivity matrices
- Distance matrix (as in BayArea), if you think $\text{Prob}(\text{dispersal/founder event}) \sim \text{distance}$
- Area size list (as in SHIBA, Webb & Ree 2011), if you think $\text{Prob}(\text{extinction event}) \sim \text{area size}$



Ancestral state (ancestral range) estimation:

LAGRANGE does marginal ancestral state estimates (fix each state, then re-optimize)

BioGeoBEARS does the above, as well as global ancestral state estimates (which may be more accurate as well as faster; Mooers 2004, *SysBio*)

BioGeoBEARS :

Forward simulations under your model

Display & summary functions

Try it here:

<http://phylo.wikidot.com/biogeobears>

