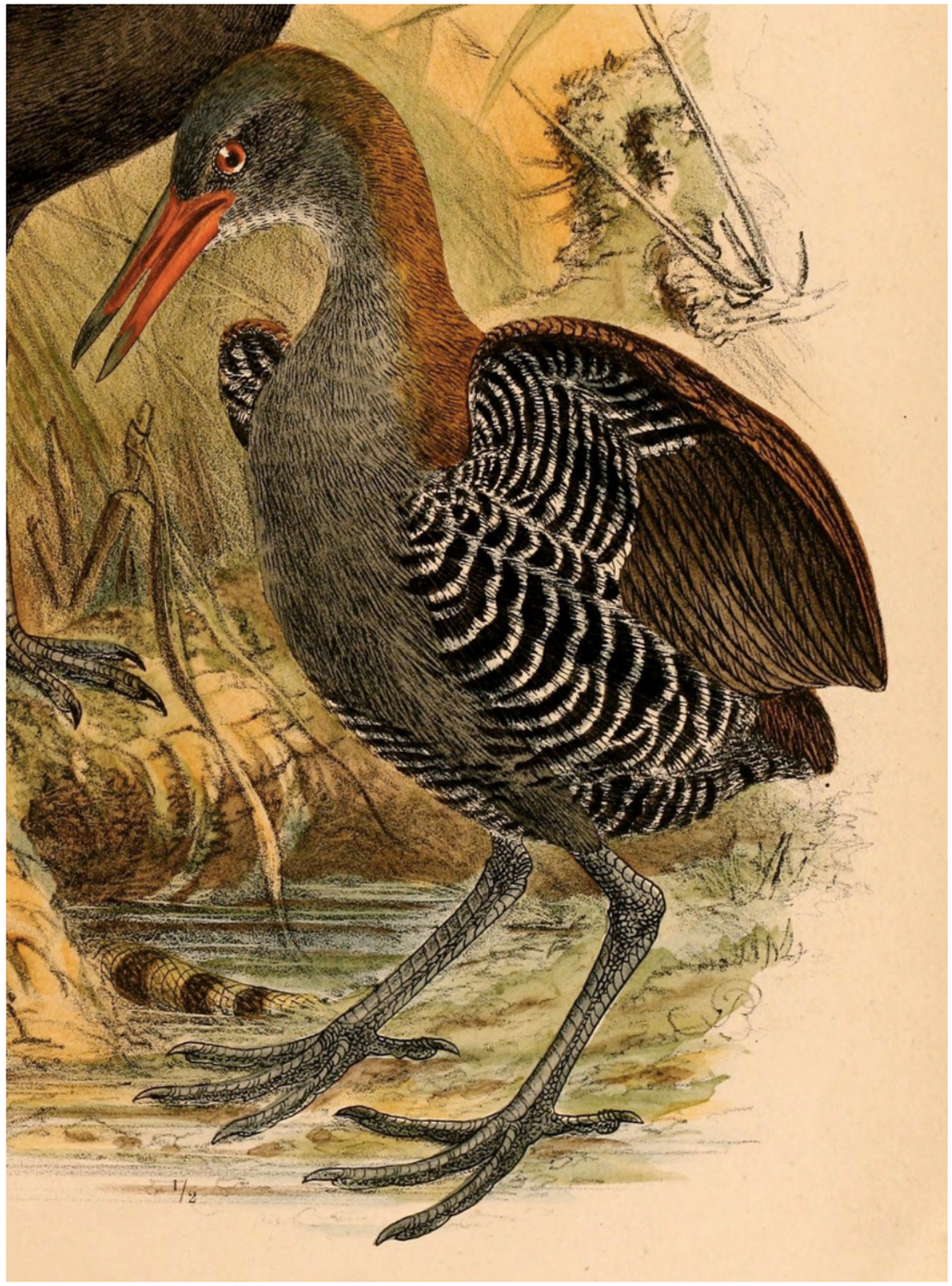
Trait-dependent dispersal models for phylogenetic biogeography, in the R package '*BioGeoBEARS*'



Snoring rail, *Aramidopsis plateni* (flightless, Sulawesi)

Adolf Meyer (1898), *The Birds of Celebes and the neighbouring islands*. https://en.wikipedia.org/wiki/Snoring_rail

Nicholas J. Matzke, DECRA Fellow
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EEG, Research School of Biology
The Australian National University
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phylo.wikidot.com/BioGeoBEARS

–June 21, 2016, iEvoBio, 2:12 pm
–Evolution 2016, Austin, TX

Ecology & Evolutionary Biology, The University of Tennessee, Knoxville

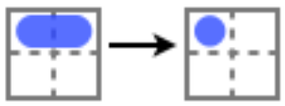
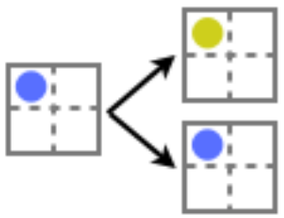
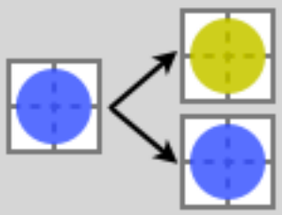
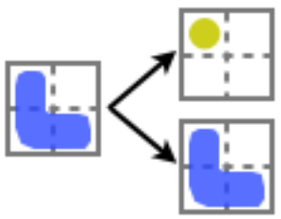
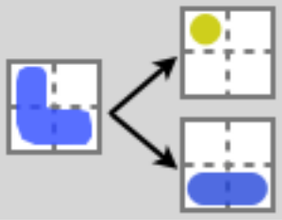
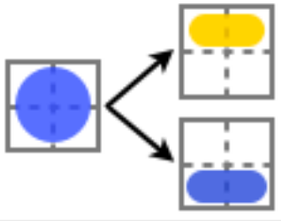
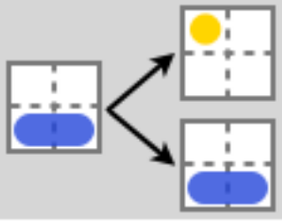
The University of California

The University of Tennessee, Knoxville

NIMBioS National Institute for Mathematical and Biological Synthesis

The Australian National University

Center for Theoretical Evolutionary Genomics
Bachtrog • Eisen • Hallatschek • Huelsenbeck • Nielsen • Slatkin • Song

	Process	Ranges (Before → After)	Character mapping	DIVA	DEC (LAGRANGE)	BayArea, BBM (RASP)	Par Biol Su
Anagenetic	Dispersal			✓	✓	✓	
	Extinction			✓	✓	✓	
	Range-switching		✓				
Cladogenetic	Sympatry (narrow)		✓	✓	✓	✓	
	Sympatry (widespread)					✓	
	Sympatry (subset)				✓		
	Vicariance (narrow)			✓	✓		
	Vicariance (widespread)			✓			
	Founder						

BioGeoBEARS supermodel can produce various submodels

Figure 1, Matzke 2013, *Frontiers of Biogeography*

Additional models in *BioGeoBEARS*

- Connectivity matrices
- User-specified dispersal probability multipliers
- Geographic distance matrices
- Environmental distance matrices
- Any of these can be "time-stratified"
- Appearing/disappearing areas

All code online at:

http://phylo.wikidot.com/BioGeoBEARS

These models leave out traits!

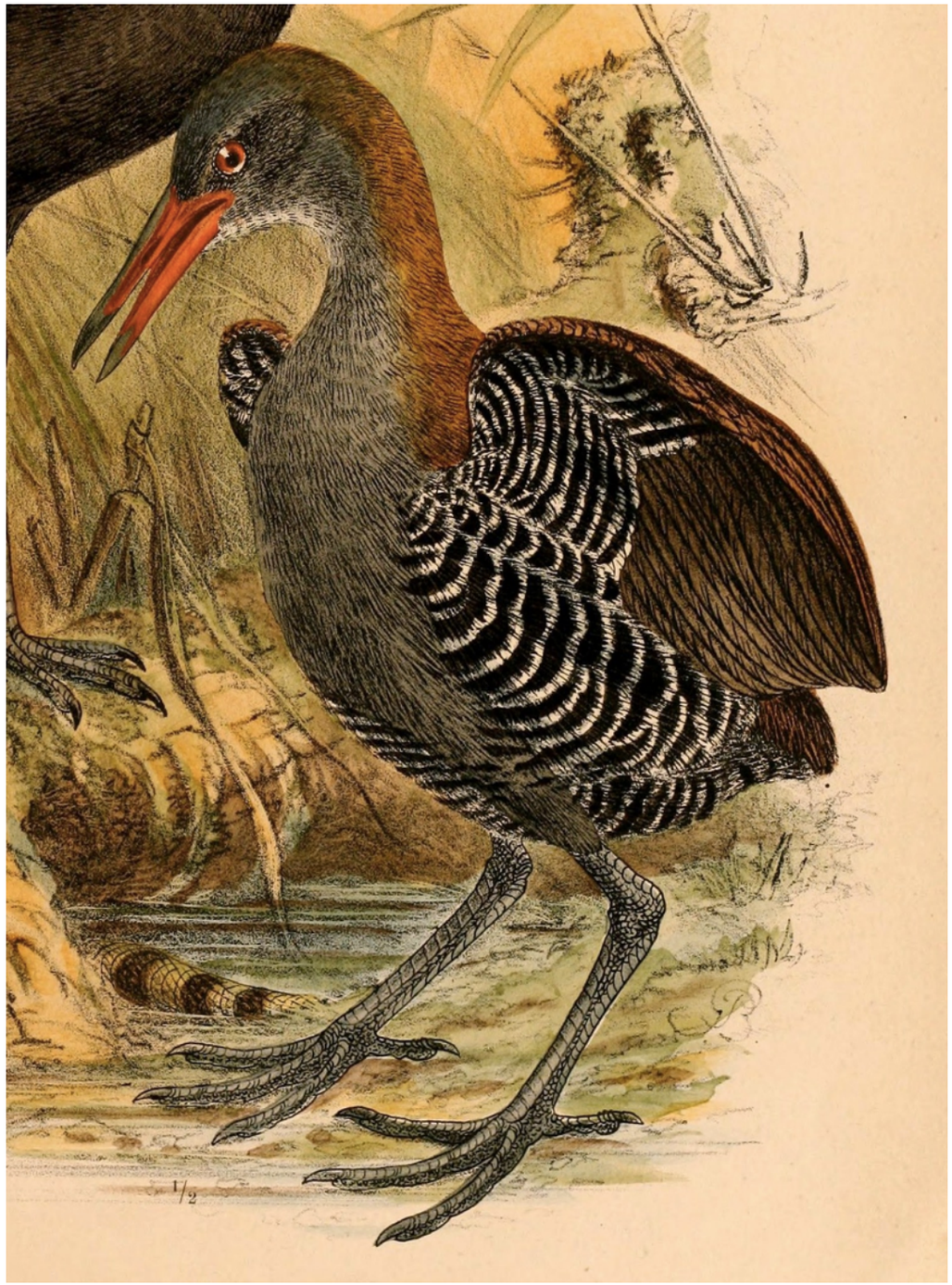
- All of the models discussed so far assume the dispersal rate is constant across the tree

- (might be modified by distance or connectivity, but not by the lineage)

- It's GOT to be important
  - Seed dispersal syndromes
  - Rafting & colonization ability
  - Flying/nonflying, etc.

Case study: Pacific Rails

"Typical Rails"



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Data from:

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Living and extinct Rail distributions (Kirchman 2012)

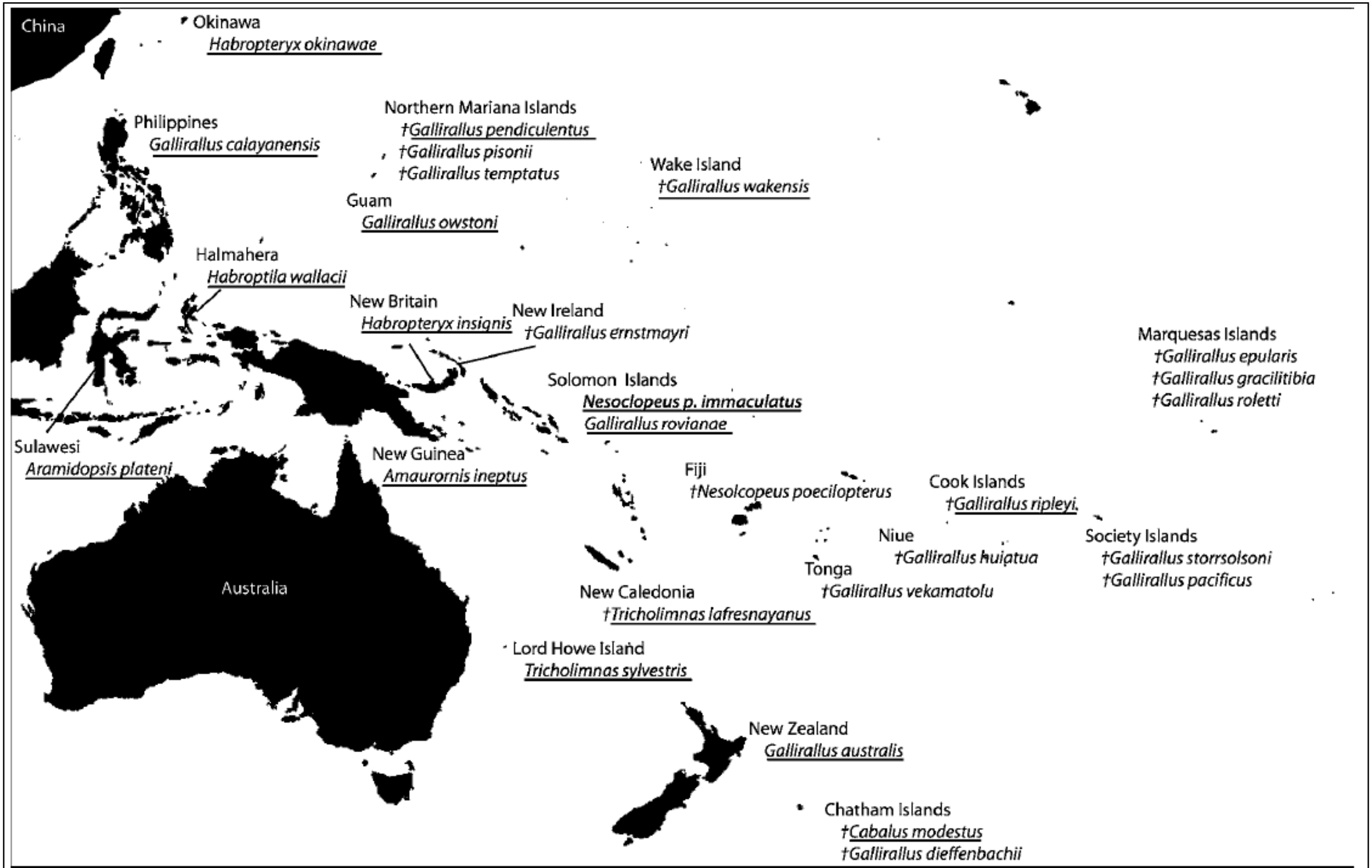

FIG. 1. Map showing the distribution of all known living and extinct (†) flightless species of "typical" rails from Pacific islands. The ranges of the volant

Source: Kirchman, Jeremy J. (2012). Speciation of Flightless Rails on Islands: A DNA-Based Phylogeny of the Typical Rails of the Pacific, *The Auk*, 129(1):56-69.

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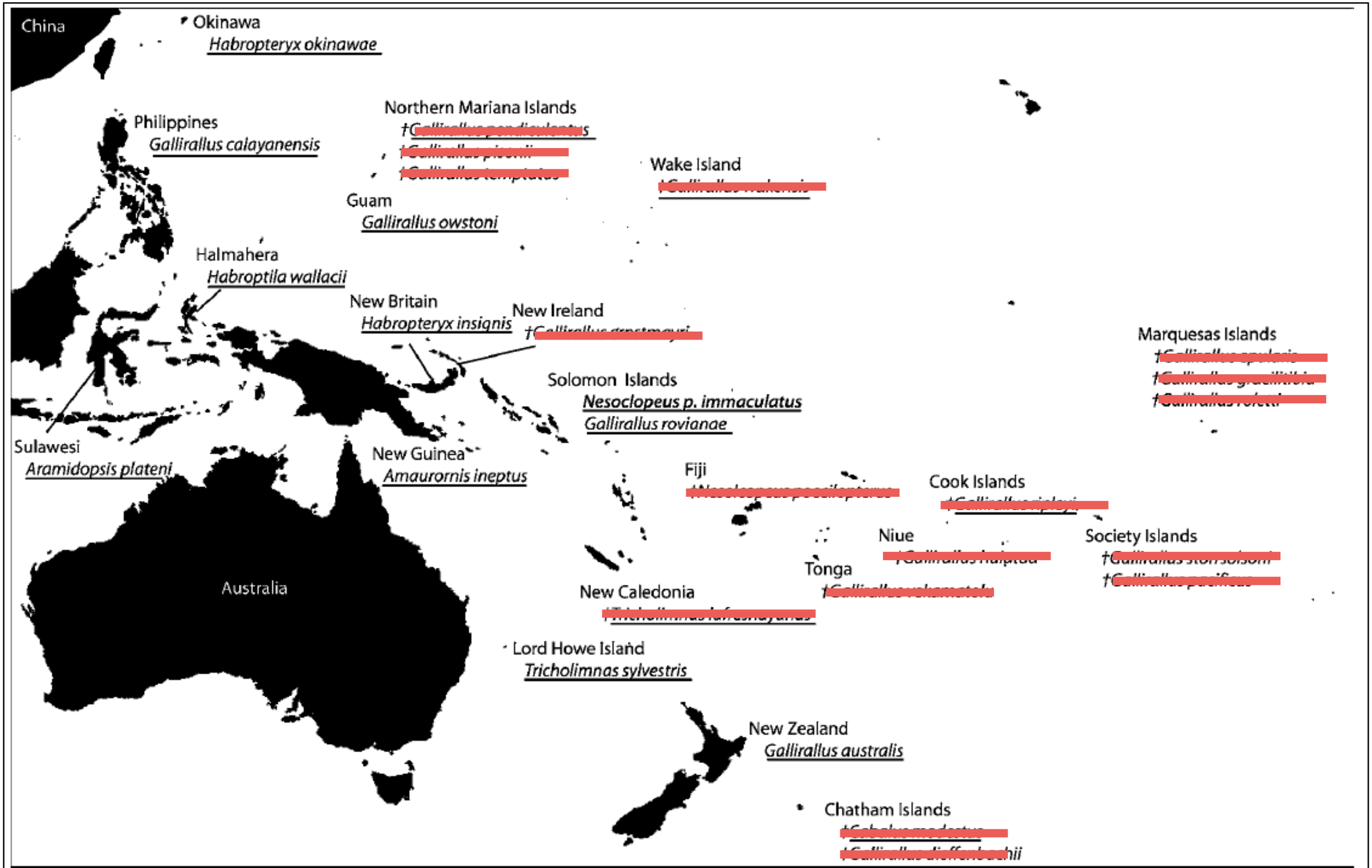

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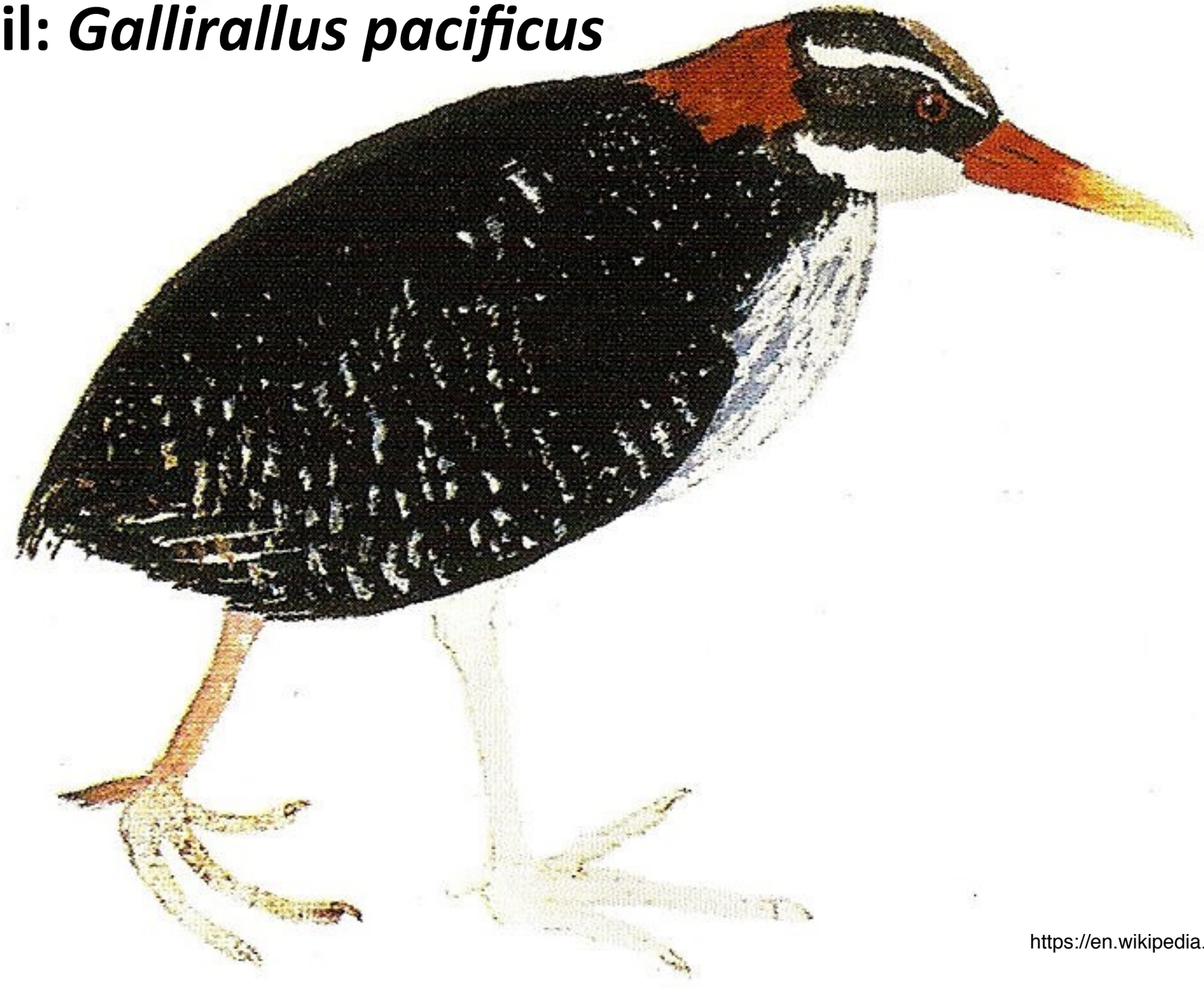
Tahiti Rail: *Gallirallus pacificus*



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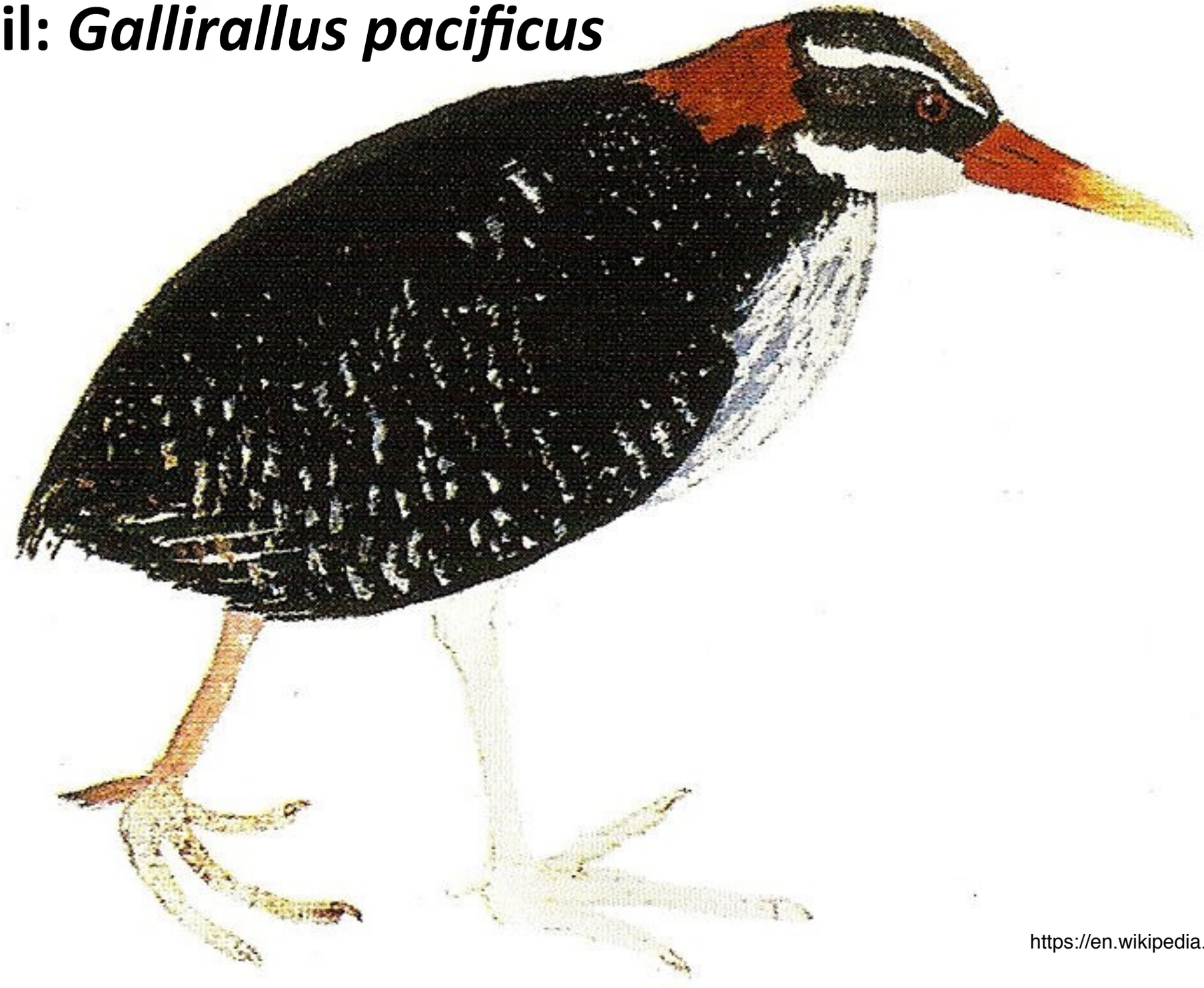
Tahiti Rail: *Gallirallus pacificus*



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(4) †*G. pacificus* of Tahiti, known only from a painting made by Georg Forster on James Cook's second voyage.

Source: Kirchman, Jeremy J. (2012). Speciation of Flightless Rails on Islands: A DNA-Based Phylogeny of the Typical Rails of the Pacific, *The Auk*, 129(1):56-69.

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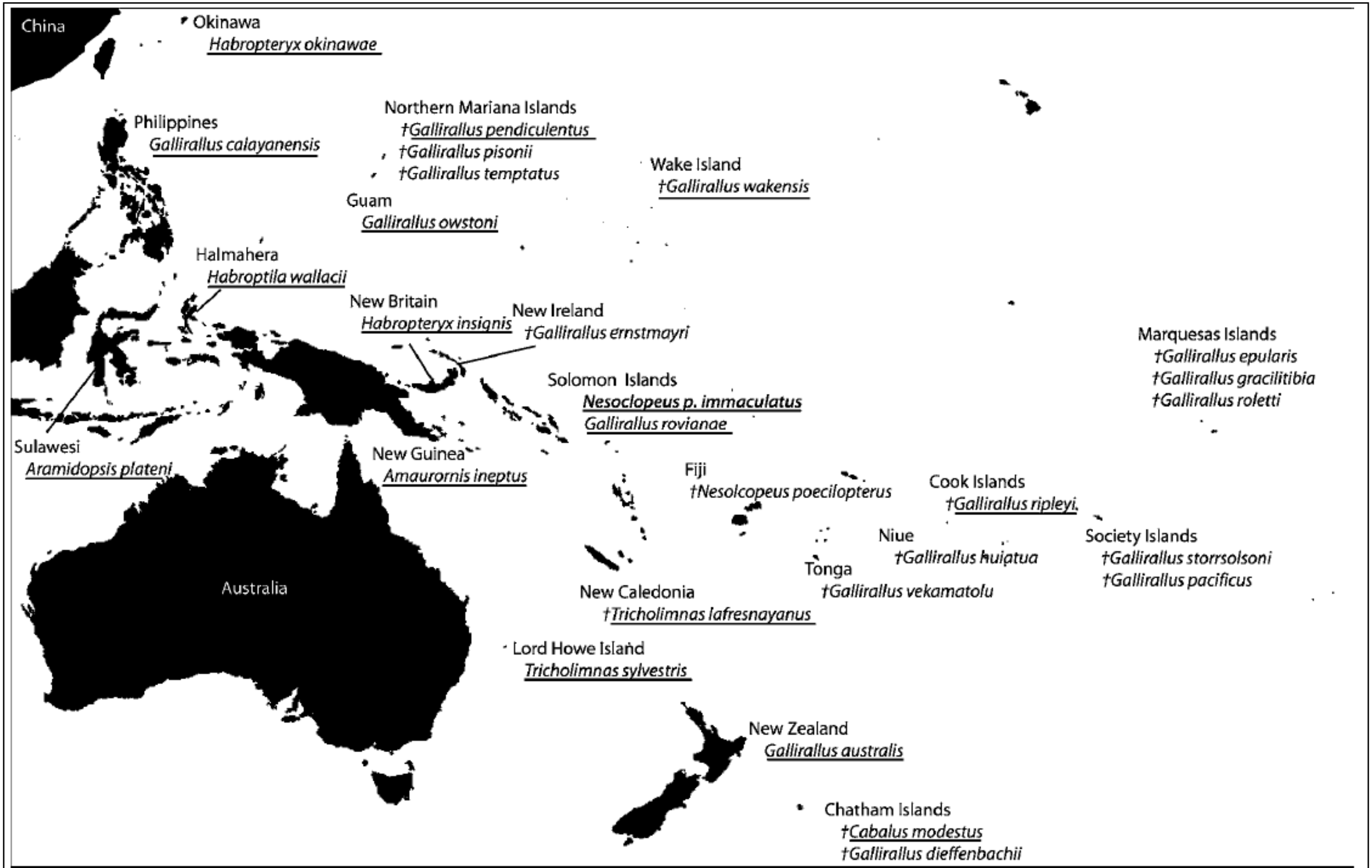

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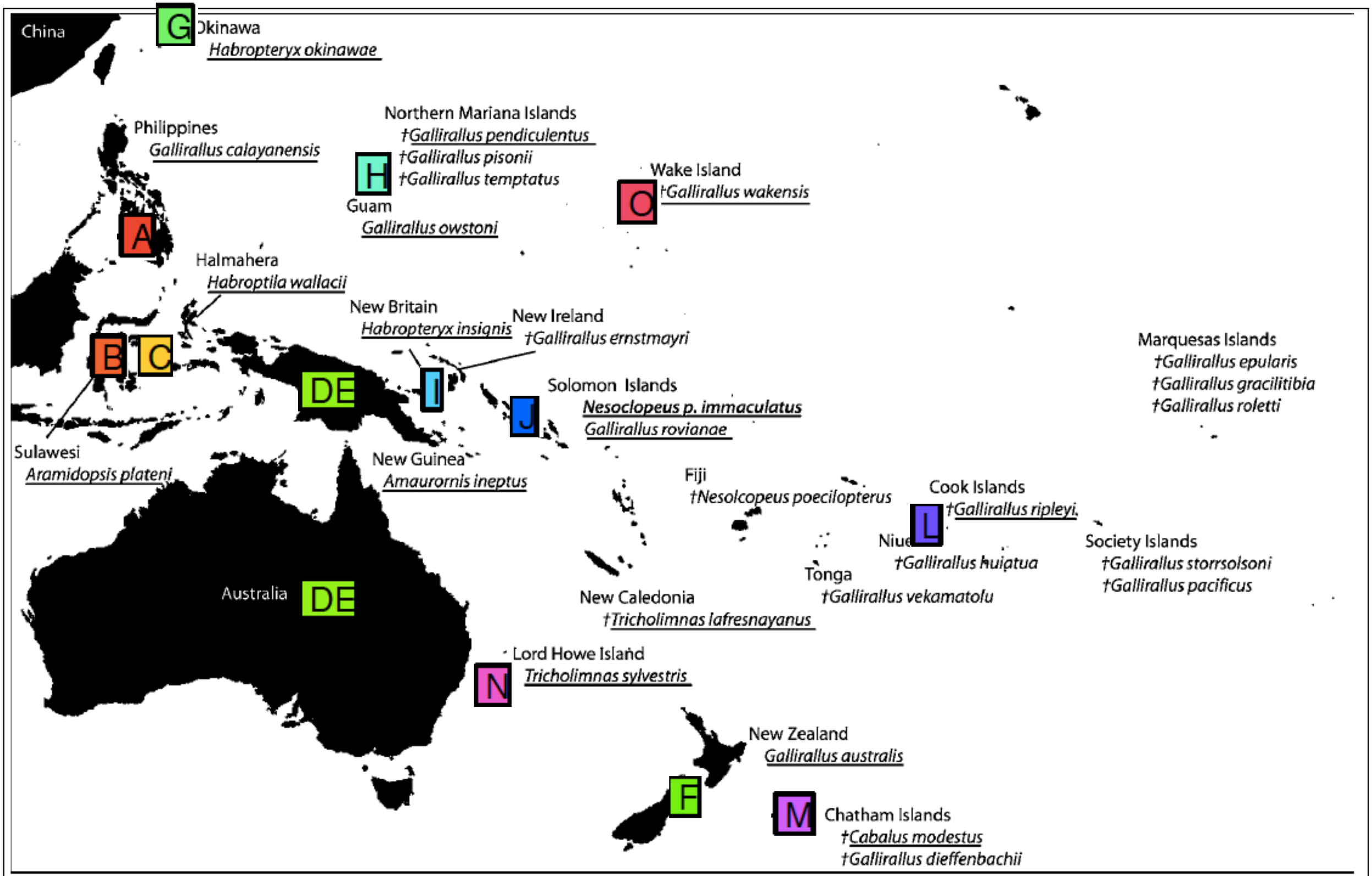
Areas (simplified from Kirchman)



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Source: Kirchman, Jeremy J. (2012). Speciation of Flightless Rails on Islands: A DNA-Based Phylogeny of the Typical Rails of the Pacific, *The Auk*, 129(1):56-69.

Areas (simplified from Kirchman)

- A Phillipines
- B Sulawesi
- C Mollucas
- DE PNG, Australia
- F New Zealand
- G Okinawa
- H Guam/Marianas
- I New Britain
- J Solomon Islands
- L Cook Islands
- M Chatham Islands
- N Lord Howe Island
- O Wake Island

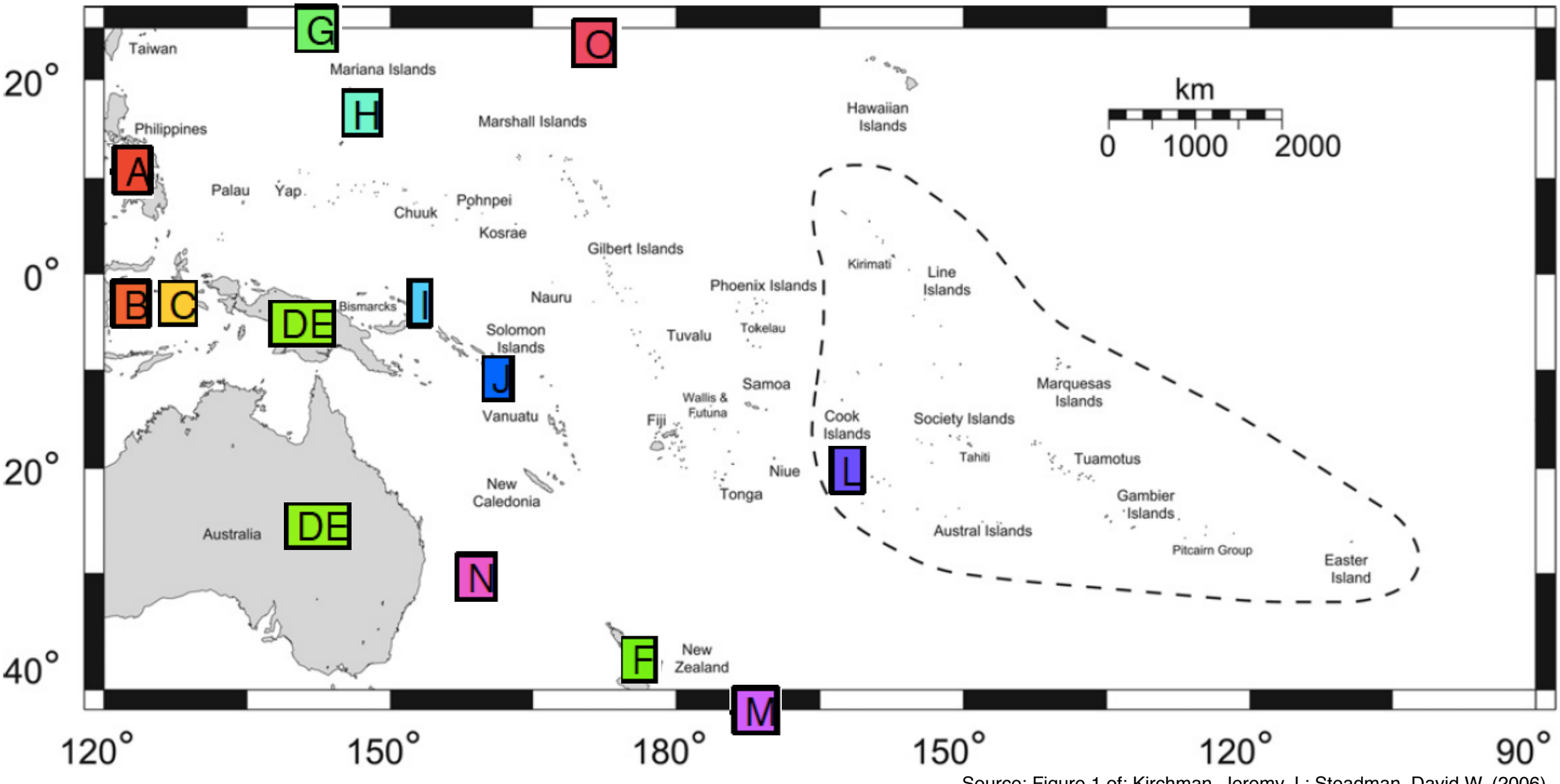
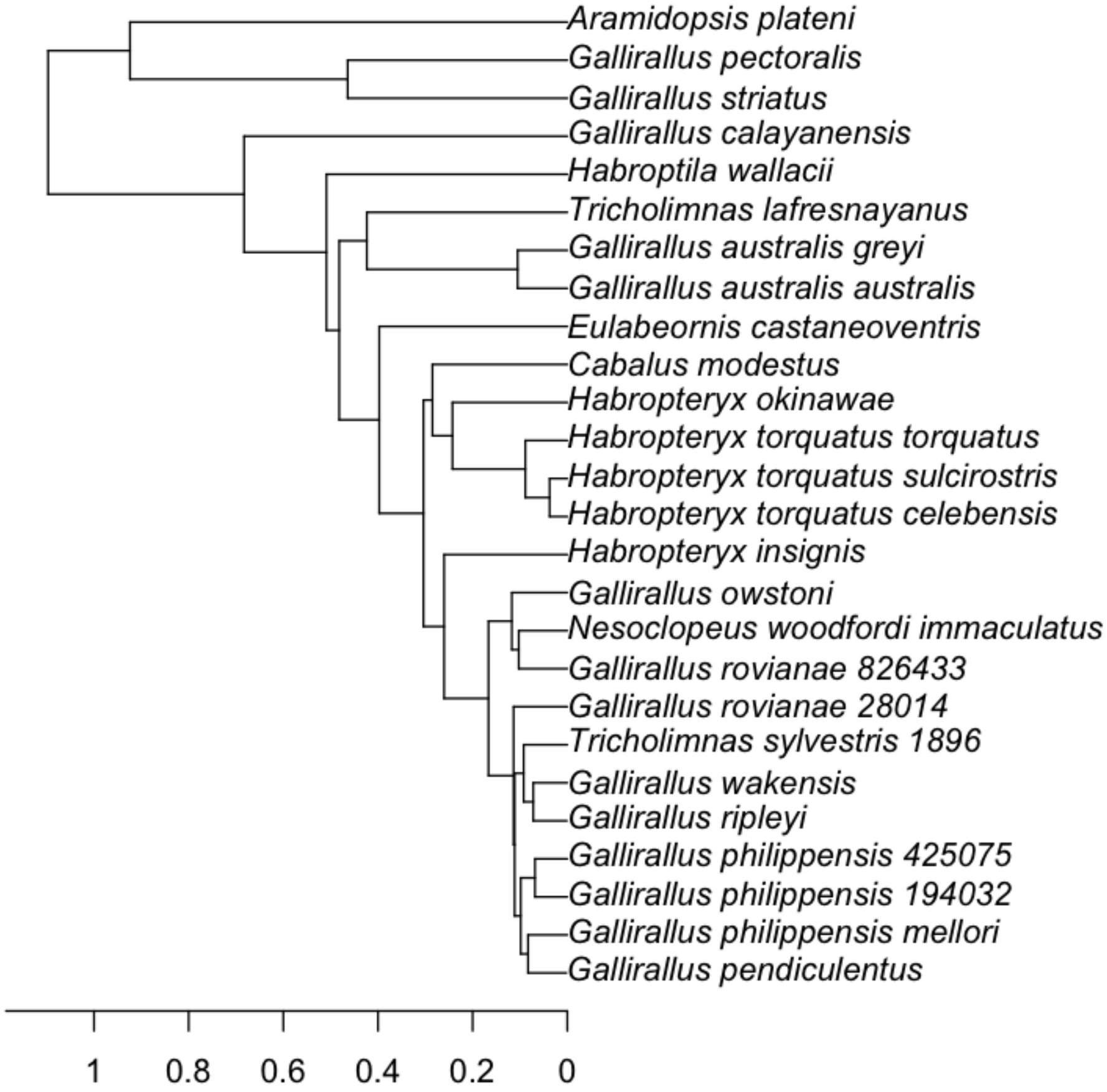


FIGURE 1. Oceania. Dashed line indicates the East Polynesia faunal region.

Source: Figure 1 of: Kirchman, Jeremy J.; Steadman, David W. (2006). New Species of Rails (Aves: Rallidae) from an Archaeological Site on Huahine, Society Islands. *Pacific Science* (2006), 60:2, 281–297.

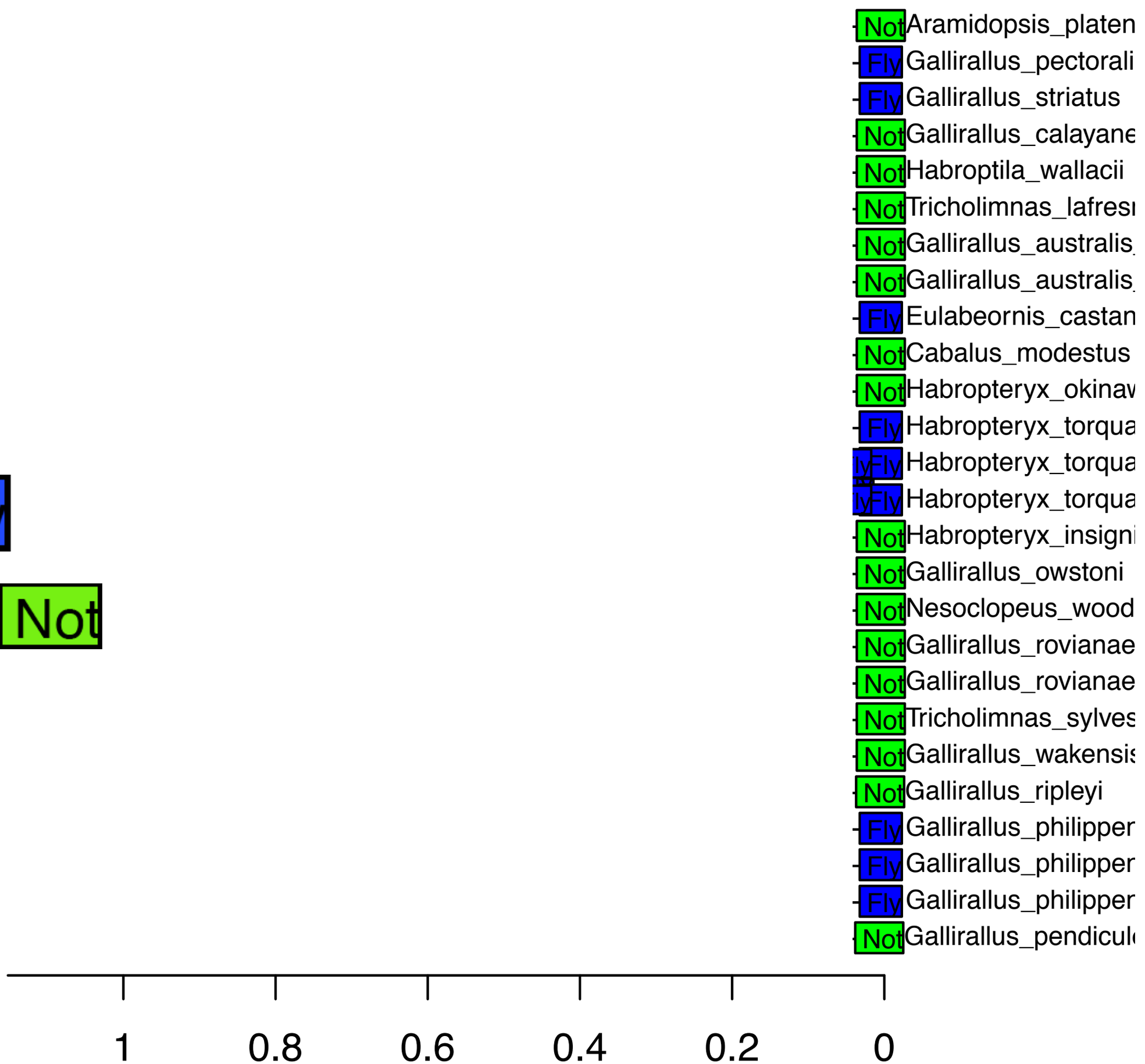
Dated phylogeny of typical Rails (simplified from Kirchman)



Distribution of flight in Pacific Rails

Flying: Fly

Non-flying: Not

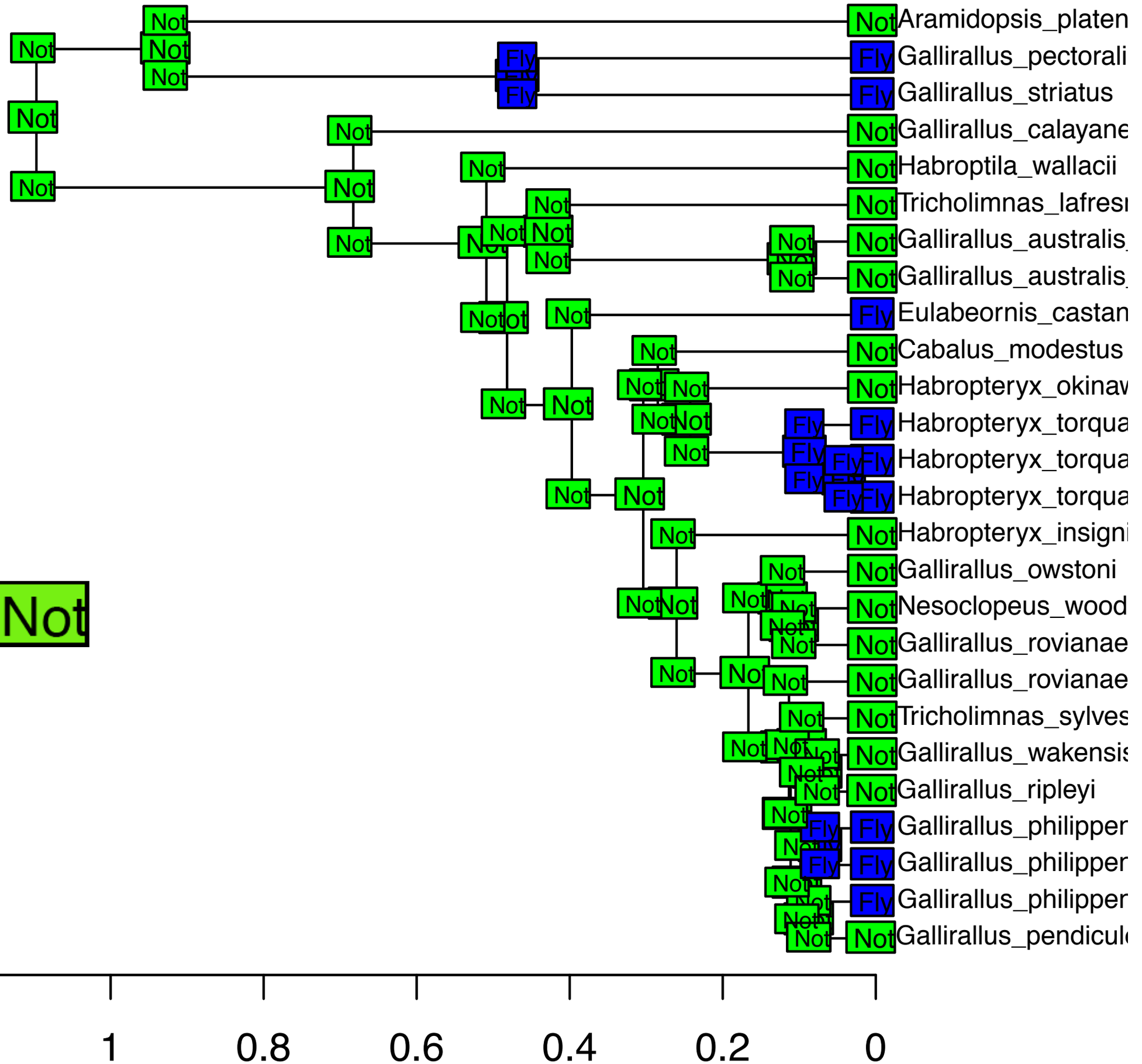


Distribution of flight in Pacific Rails

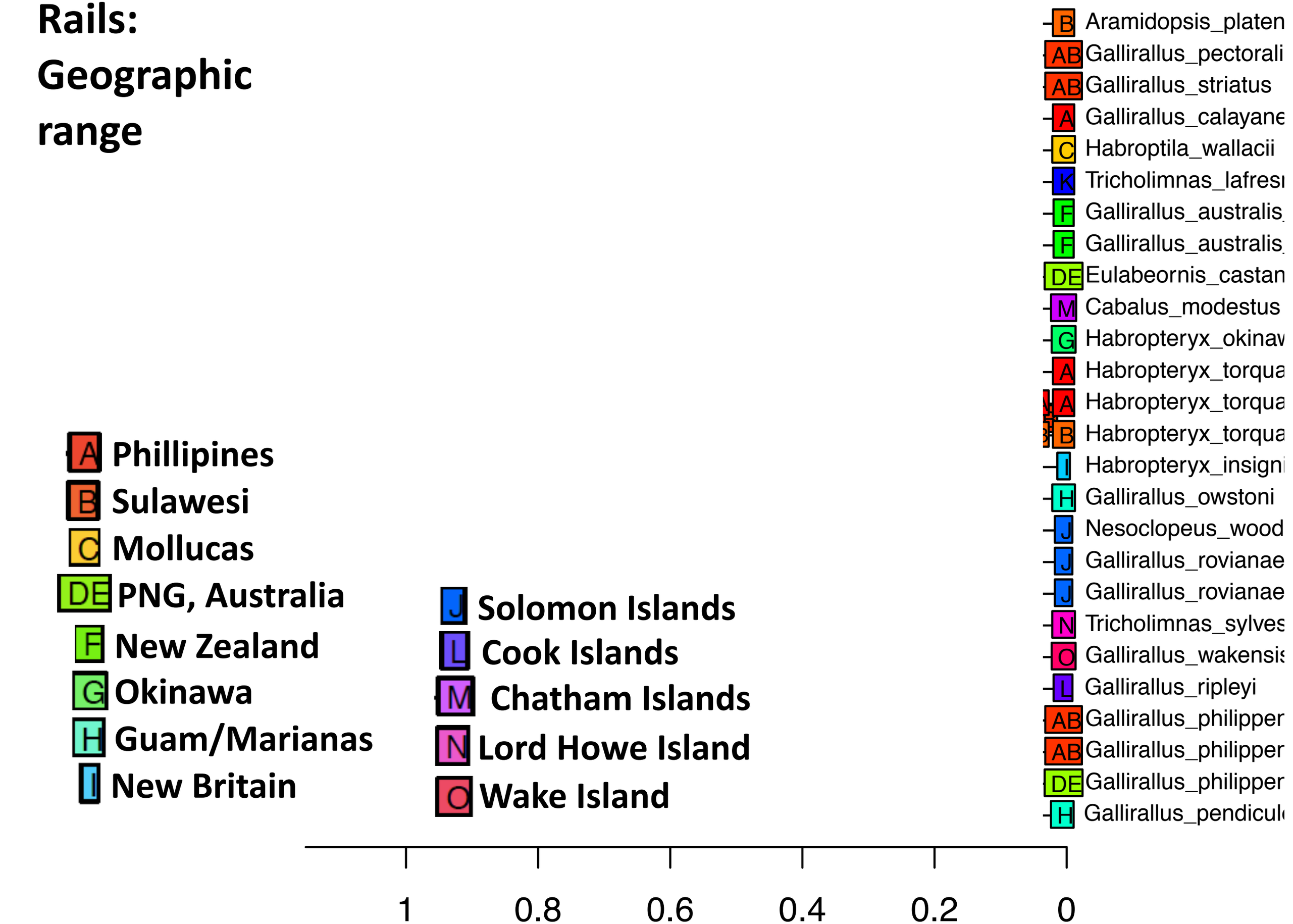
(standard trait model)

Flying: Fly

Non-flying: Not



Rails: Geographic range



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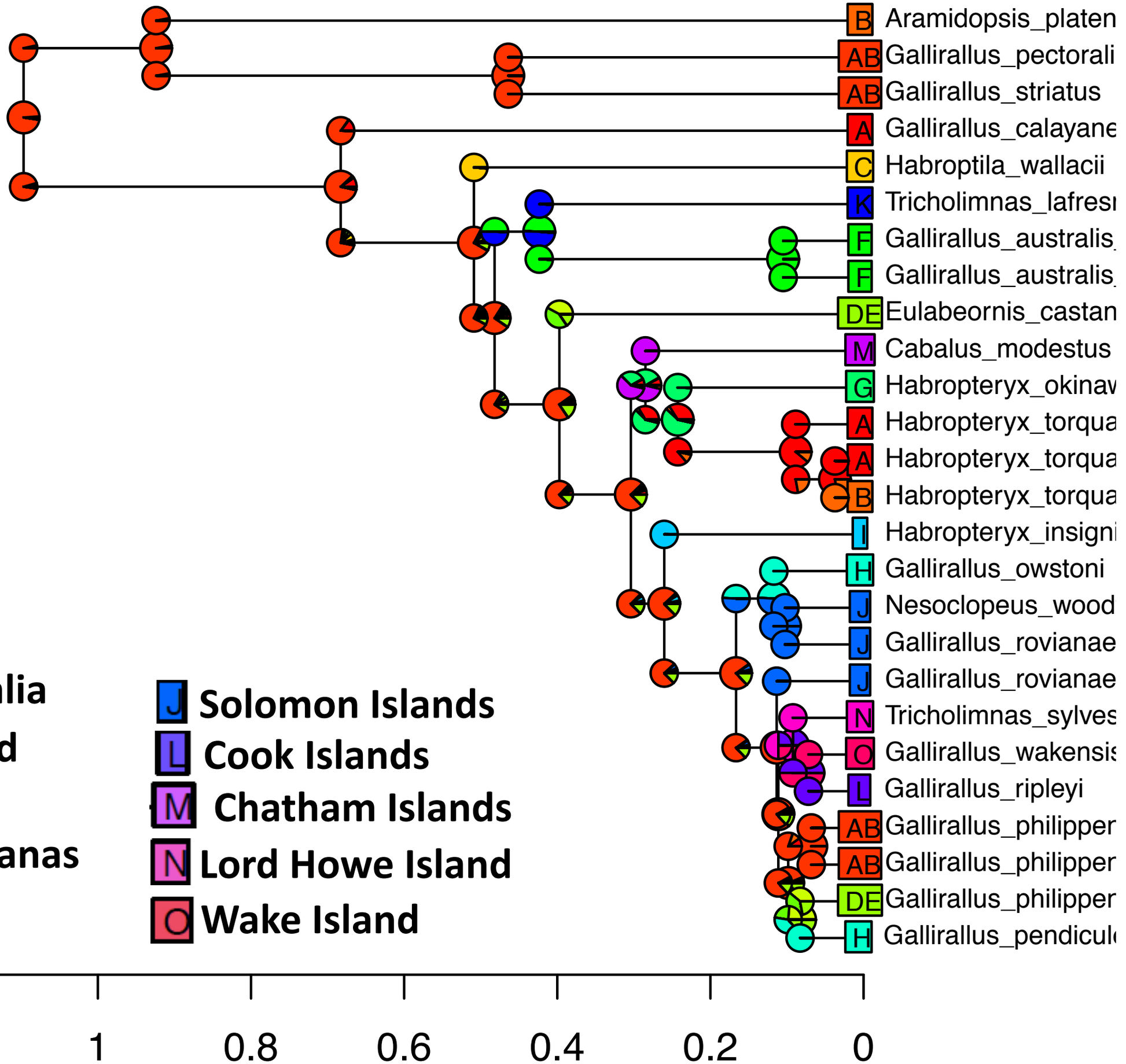


A Phillipines
B Sulawesi
C Mollucas
DE PNG, Australia
F New Zealand
G Okinawa
H Guam/Marianas
I New Britain
J Solomon Islands
L Cook Islands
M Chatham Islands
N Lord Howe Island
O Wake Island

Clearly the group has dispersed

…but probably they were flying to do it!

Build a trait-based dispersal model

1. Trait flight/flightlessness trait evolves on tree

   Parameters of model:

Clearly the group has dispersed

…but probably they were flying to do it!

Build a trait-based dispersal model

1. Trait flight/flightlessness trait evolves on tree

   Parameters of model:

   t12 -> Rate of flight loss

   t21 -> Rate of flight gain

   m2 -> Multiplier on dispersal prob. while flightless

Clearly the group has dispersed

…but probably they were flying to do it!

Build a trait-based dispersal model

1. Trait flight/flightlessness trait evolves on tree

Parameters of model:

t12 -> Rate of flight loss

t21 -> Rate of flight gain

m2 -> Multiplier on dispersal prob. while flightless

	FLY	NOT
FLY	-	t12
NOT	t21	-

Clearly the group has dispersed

…but probably they were flying to do it!

Build a trait-based dispersal model

1. Trait flight/flightlessness trait evolves on tree

   Parameters of model:

   t12 -> Rate of flight loss

   t21 -> Rate of flight gain

   m2 -> Multiplier on dispersal prob. while flightless

	FLY	NOT
FLY	-	t12
NOT	t21	-

2. Combine trait model with anagenetic dispersal

Clearly the group has dispersed

…but probably they were flying to do it!

Build a trait-based dispersal model

3. Cladogenetic parameters of model:

jt12 -> Chance of “jumping” from flight-> flightless during founder-event speciation

Trait-dependent **DEC model**

Traditional:

Dispersal-Extinction (on branches)

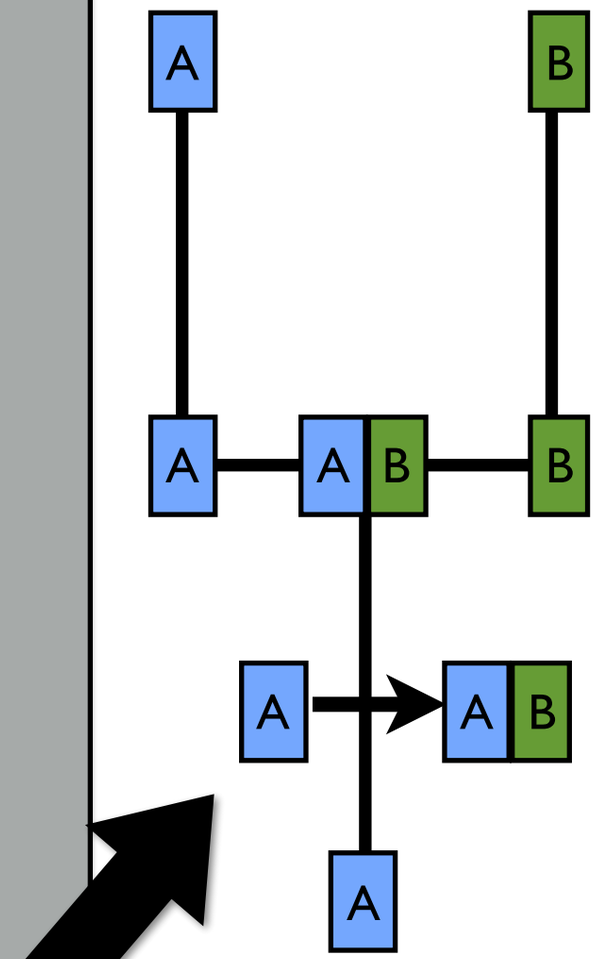
d = rate of "dispersal" (range expansion)

e = rate of "extinction" (range contraction / local extirpation)

Rate matrix:

descendant range

ancestor range	***null***	**A**	**B**	**AB**
null	-			
A	*e*	-		*d*
B	*e*		-	*d*
AB		*e*	*e*	-



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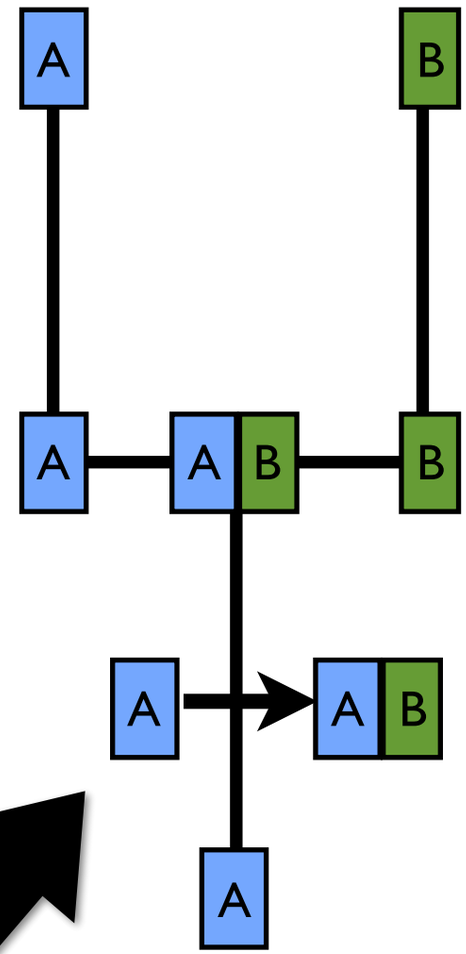
B	*e*		-	*d*
AB		*e*	*e*	-



Trait-dependent:

Rate matrix:

Trait-dependent **DEC model**

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Rate matrix:

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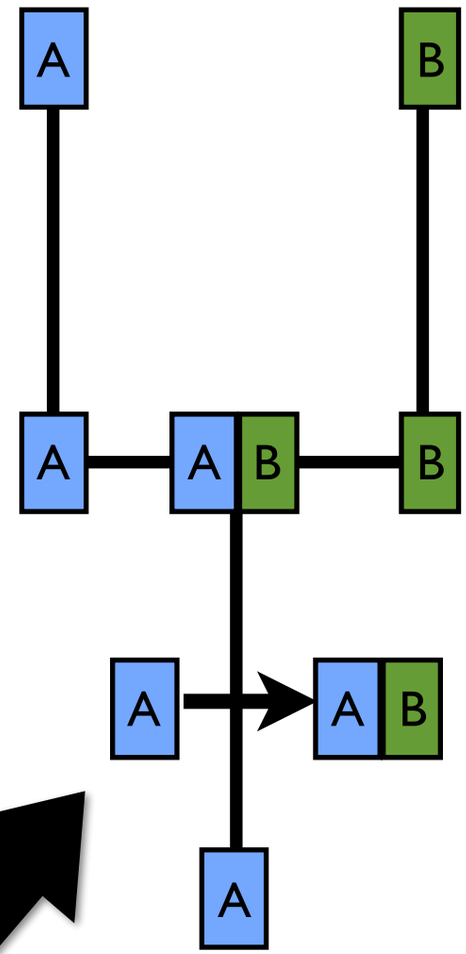
null	-			
A	*e*	-		*d*
B	*e*		-	*d*
AB		*e*	*e*	-



Trait-dependent:

Rate matrix:

	FLY	NOT
FLY	-	t12
NOT	t21	-

Trait-dependent **DEC model**

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Dispersal-Extinction (on branches)

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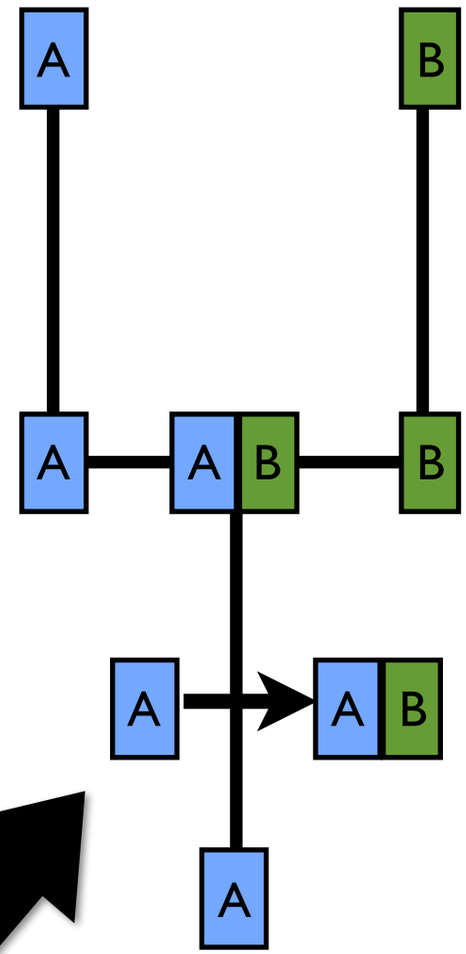
ancestor range \ descendant range	*null*	A	B	AB
null	-			
A	*e*	-		*d*
B	*e*		-	*d*
AB		*e*	*e*	-



Trait-dependent:

Rate matrix:

	FLY	NOT
FLY	-	t12
NOT	t21	-

ancestor range \ descendant range	*null*	A	B	AB
null	-			
A	*e*	-		*d*
B	*e*		-	*d*
AB		*e*	*e*	-

trait matrix + dispersal/extinction

	FLY	NOT
FLY	-	t12
NOT	t21	-

+

ancestor range

descendant range

	null	A	B	AB
null	-			
A	*e*	-		*d*
B	*e*		-	*d*
AB		*e*	*e*	-

=

trait matrix + dispersal/extinction

	FLY	NOT
FLY	-	t12
NOT	t21	-

+

ancestor range

descendant range

	null	A	B	AB
null	-			
A	*e*	-		*d*
B	*e*		-	*d*
AB		*e*	*e*	-

=

Combined anagenetic matrix

	null	A	B	AB
null	-			
A	*e*	-		***d***
B	*e*		-	***d***
AB		*e*	*e*	-

t12

t21

	null	A	B	AB
null	-			
A	*e*	-		***md***
B	*e*		-	***md***
AB		*e*	*e*	-

DEC+J model: add trait to jump

(Matzke 2014)

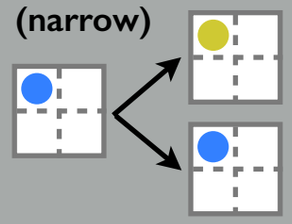
Traditional:

Cladogenesis (at splits)

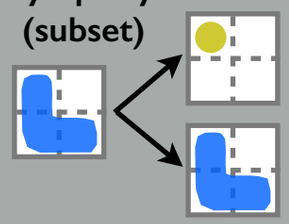
Equal per-event weights

(modified by *j* in DEC+J)

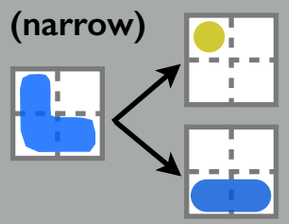
Sympatry (narrow)



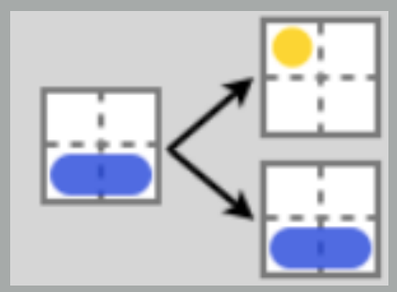
Sympatry (subset)

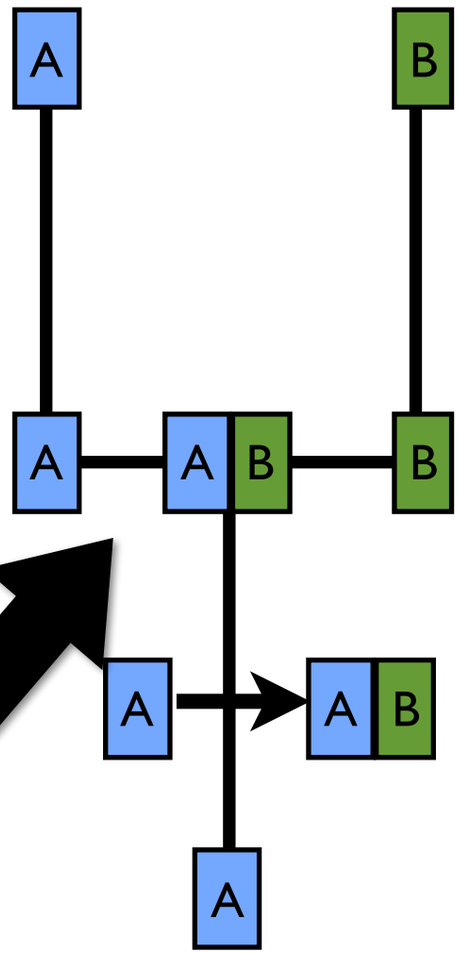


Vicariance (narrow)



Jump dispersal (founder events)





DEC+J model: add trait to jump

(Matzke 2014)

Traditional:

Trait-dependent:

Cladogenesis (at splits)

Sympatry (narrow)

Equal per-event weights

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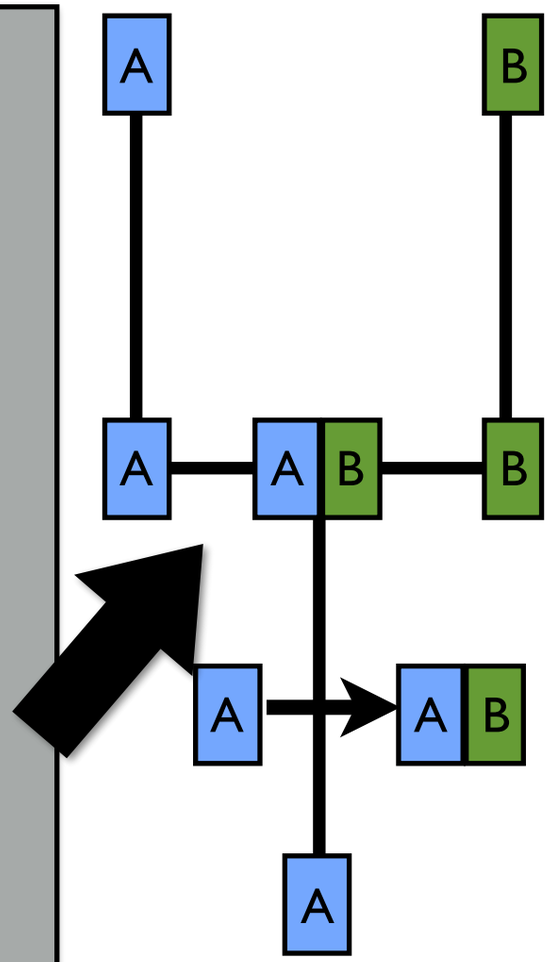
Sympatry (subset)

Jump dispersal (founder events)

Vicariance (narrow)



Cladogenesis (at splits)

DEC+J model: add trait to jump

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Traditional:

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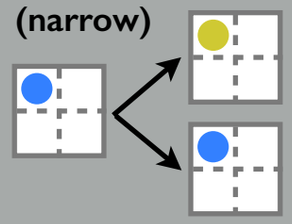
Cladogenesis (at splits)

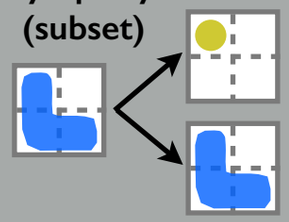
Sympatry (narrow)



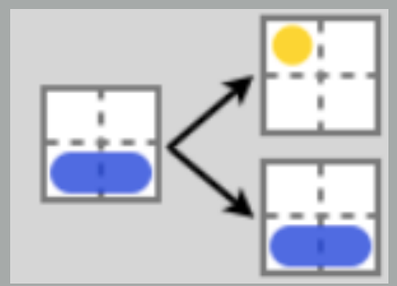
Equal per-event weights

(modified by *j* in DEC+J)

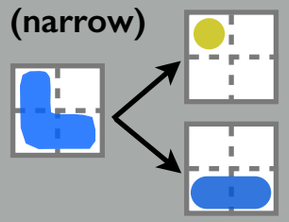
Sympatry (subset)

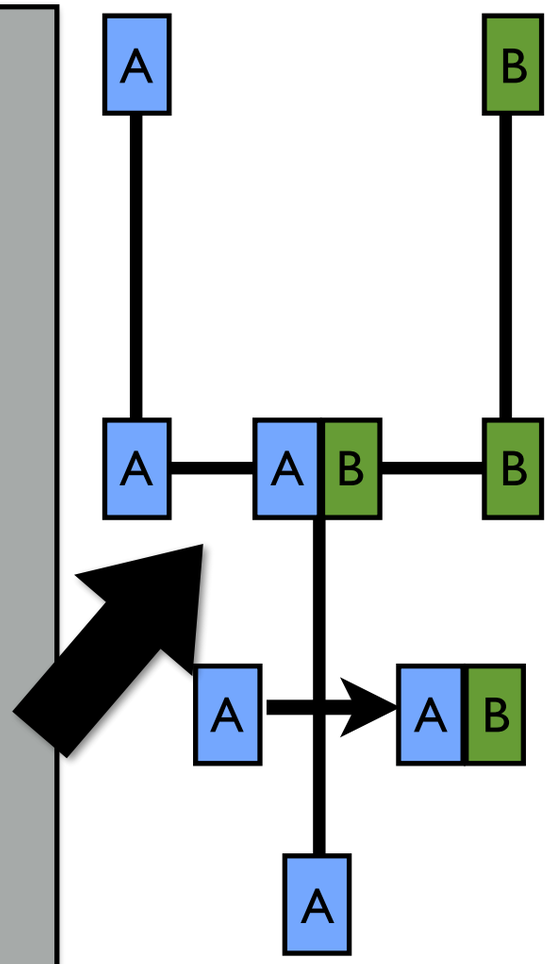


Jump dispersal (founder events)



Vicariance (narrow)





Cladogenesis (at splits)

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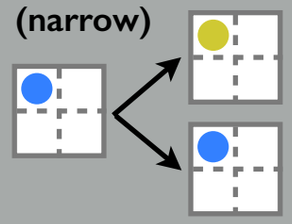
(Matzke 2014)

Traditional:

Cladogenesis (at splits)

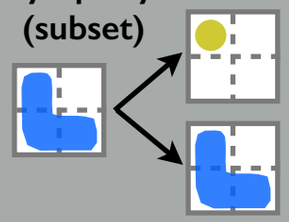
Sympatry (narrow)



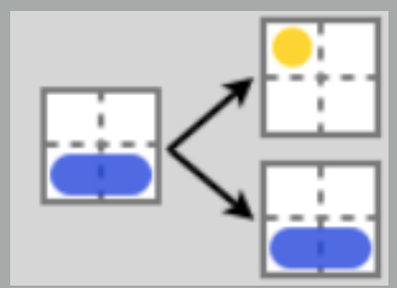
Equal per-event weights

(modified by *j* in DEC+J)

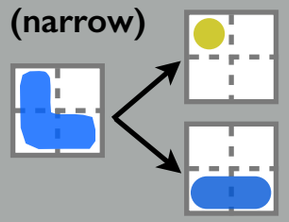
Sympatry (subset)

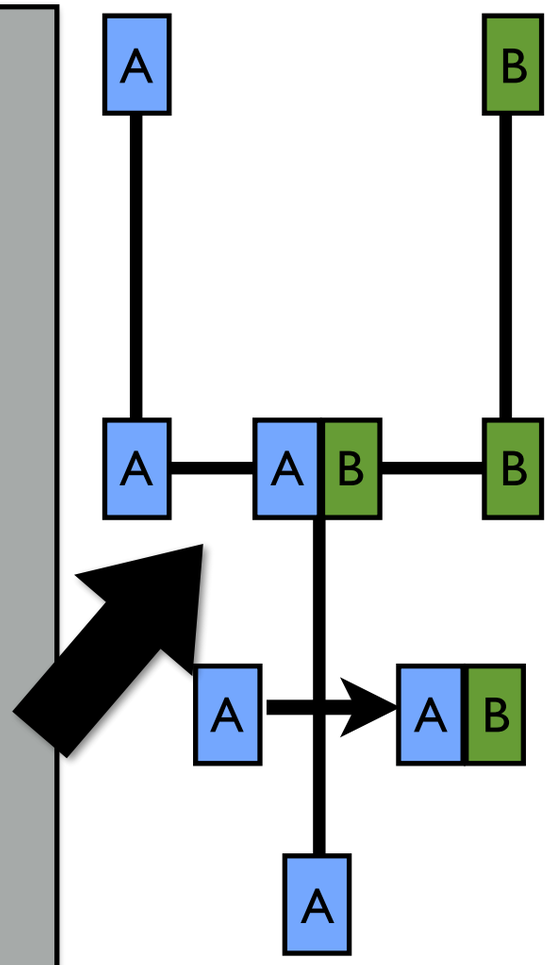


Jump dispersal (founder events)



Vicariance (narrow)





Trait-dependent:

Cladogenesis (at splits)

Trait model:

DEC+J model: add trait to jump

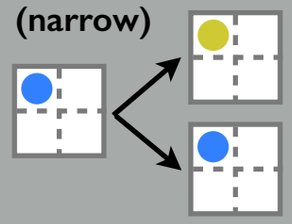
(Matzke 2014)

Traditional:

Trait-dependent:

Cladogenesis (at splits)

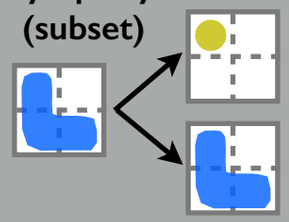
Sympatry (narrow)



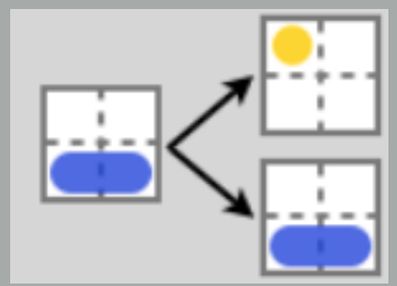
Equal per-event weights

(modified by *j* in DEC+J)

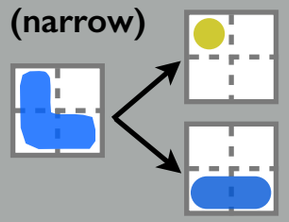
Sympatry (subset)

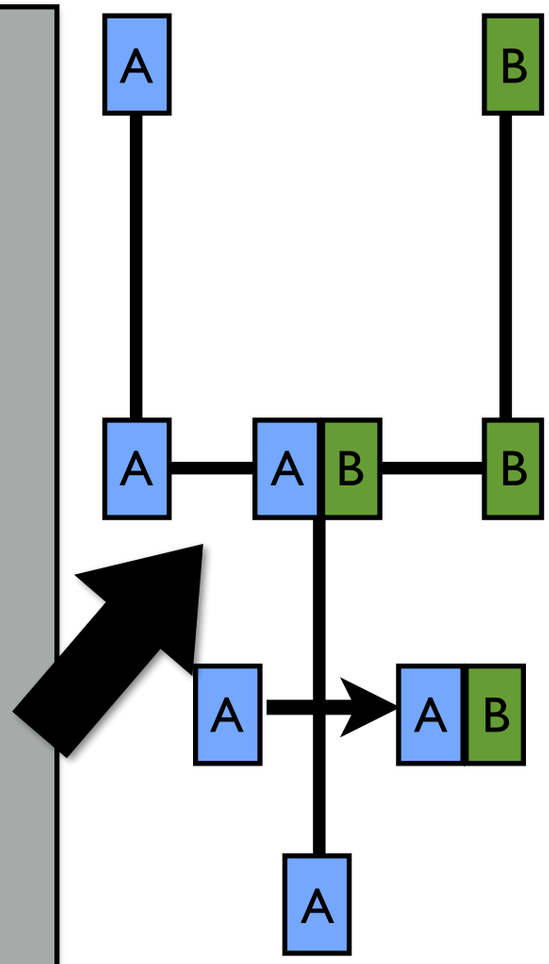


Jump dispersal (founder events)



Vicariance (narrow)





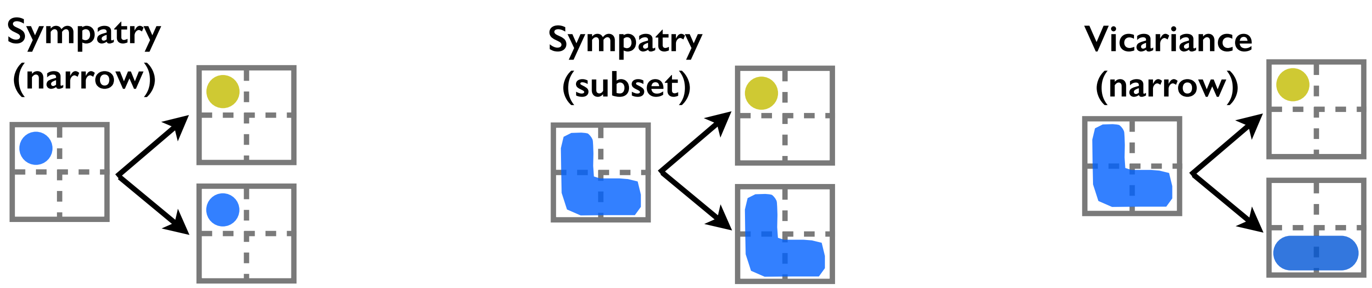
Cladogenesis (at splits)

Trait model:

***m2* x**

Cladogenetic range-change model: DEC

Cladogenetic range-change events:



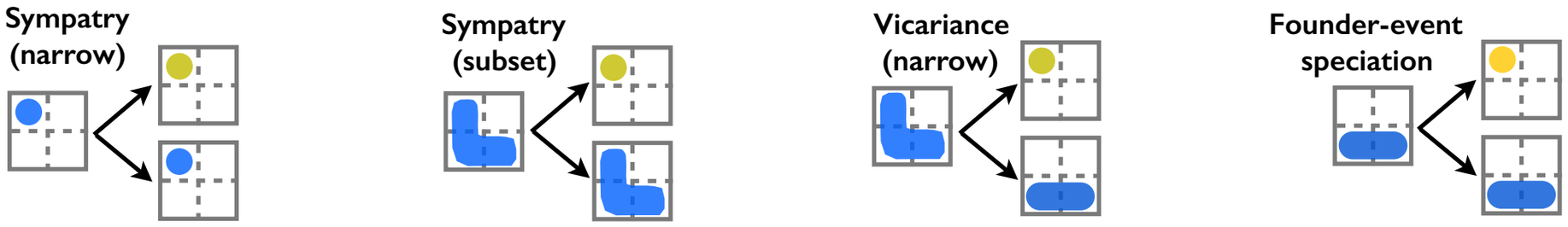
Cladogenetic transition matrix:

ending range

left:	A	A	A	A	A	A	A	B	B	B	B	B	B	B	C	C	C	C	C	C	C	AB	AB	AB	AB	AB	AB	AB	BC	BC	BC	BC	BC	BC	BC	AC	AC	AC	AC	AC	AC	AC	ABC	ABC	ABC	ABC	ABC	ABC	ABC	
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**	**BC**	**AC**	**ABC**	**A**	**B**	**C**	**AB**	**BC**	**AC**	**ABC**	**A**	**B**	**C**	**AB**	**BC**	**AC**	**ABC**	**A**	**B**	**C**	**AB**	**BC**	**AC**	**ABC**	**count**
A	sym																																																	1
B									sym																																									1
starting C																	sym																																	1
range AB		vic		sub				vic			sub											sub	sub																											6
BC										vic		sub				vic			sub											sub	sub																			6
AC			vic			sub									vic					sub																sub		sub												6
ABC					vic		sub						vic	sub				vic			sub			vic					vic								vic						sub	sub	sub					12

Cladogenetic range-change model: DEC+J

Cladogenetic range-change events:



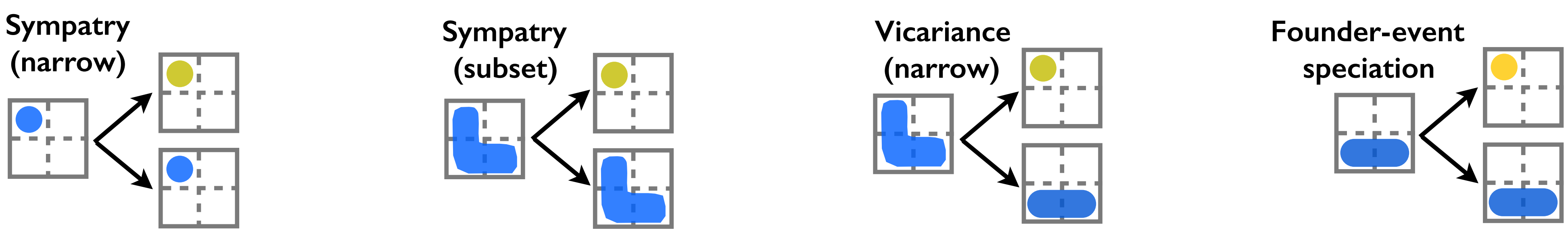
Cladogenetic transition matrix:

ending range

	left:	A	A	A	A	A	A	A	B	B	B	B	B	B	B	C	C	C	C	C	C	C	AB	AB	AB	AB	AB	AB	AB	BC	BC	BC	BC	BC	BC	BC	AC	AC	AC	AC	AC	AC	AC	ABC	ABC	ABC	ABC	ABC	ABC	ABC	
	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	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	**count**
starting range	**A**	sym	**j**	**j**												**j**																																					**5**
	B		**j**						**j**	sym	**j**						**j**																																				**5**
	C			**j**							**j**					**j**	**j**	sym																																			**5**
	AB		vic		sub				vic			sub							**j**				sub	sub	**j**																											**8**
	BC					**j**					vic		sub				vic			sub										**j**	sub	sub																				**8**
	AC			vic			sub							**j**		vic					sub																sub	**j**	sub														**8**
	ABC					vic		sub						vic	sub				vic			sub								vic								vic							sub	sub	sub						**12**

Trait-based cladogenetic model: **DEC+J**

Cladogenetic range-change events:



Cladogenetic transition matrix while flying:

ending range

	left:	A	A	A	A	A	A	A	B	B	B	B	B	B	B	C	C	C	C	C	C	C	AB	AB	AB	AB	AB	AB	AB	BC	BC	BC	BC	BC	BC	BC	AC	AC	AC	AC	AC	AC	AC	ABC	ABC	ABC	ABC	ABC	ABC	ABC	
	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	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	count
	A	sym	j	j												j																																			5
	B		j						j	sym	j						j																																		5
starting	C			j							j					j	j	sym																																	5
range	AB		vic		sub				vic			sub							j				sub	sub	j																										8
	BC					j					vic		sub				vic			sub										j	sub	sub																			8
	AC			vic			sub							j		vic					sub																sub	j	sub												8
	ABC					vic		sub						vic	sub				vic			sub			vic					vic								vic						sub	sub	sub					12

Cladogenetic transition matrix while non-flying: *j* = *m* x *j*

ending range

	left:	A	A	A	A	A	A	A	B	B	B	B	B	B	B	C	C	C	C	C	C	C	AB	AB	AB	AB	AB	AB	AB	BC	BC	BC	BC	BC	BC	BC	AC	AC	AC	AC	AC	AC	AC	ABC	ABC	ABC	ABC	ABC	ABC	ABC	
	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	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	A	B	C	AB	BC	AC	ABC	count
	A	sym	mj	mj												mj																																			5
	B		mj						mj	sym	mj						mj																																		5
starting	C			mj							mj					mj	mj	sym																																	5
range	AB		vic		sub				vic			sub							mj				sub	sub	mj																										8
	BC					mj					vic		sub				vic			sub										mj	sub	sub																			8
	AC			vic			sub							mj		vic					sub																sub	j	sub												8
	ABC					vic		sub						vic	sub				vic			sub			vic					vic								vic						sub	sub	sub					12

Results: Model choice

Base model	rate of range expansion *d*	rate of range loss *e*	weight of founder-event speciation *j*	rate of flight -> flightlessness t_{12}	rate of flightlessness -> flight t_{21}	dispersal multiplier when trait=1 (flight) m_1	dispersal multiplier when trait=2 (flightless) m_2	rate of switch to flightlessness during founder event jt_{12}	rate of switch to flight during founder event jt_{21}	number of free parameters np	log-likelihood LnL	delta AICc dAICc	model weight mw
	Black: free parameter that is estimated. Gray: fixed parameter.												
DEC	3.84	1.94	0	3.31	0.94	1	0	0	0	4	-119.6	37.6	0.0%
DEC	0.18	0.00	0.28	5.18	1.65	1	0	0	0	5	-103.9	9.4	0.9%
DEC	3.81	2.01	0	2.58	0	1	0	0	0	3	-120.3	36.2	0.0%
DEC	0.15	0.00	0.16	2.84	0	1	0	0	0	4	-107.5	13.5	0.1%
DEC	2.50	1.69	0	3.60	1.28	1	0	1.00	0	5	-119.4	40.3	0.0%
DEC	0.18	0.00	0.82	4.37	1.12	1	0	0.75	0	6	-104.2	13.3	0.1%
DEC	3.31	1.98	0	2.57	0	1	0	1.00	0	4	-120.2	38.9	0.0%
DEC	0.15	1E-12	0.16	2.84	0	1	0	0.00	0	5	-107.5	16.6	0.0%
DIVALIKE	1.99	0.82	0	5.16	1.48	1	0	0	0	4	-115.2	28.9	0.0%
DIVALIKE	0.24	0.00	0.22	5.73	1.71	1	0	0	0	5	-104.1	9.8	0.7%
DIVALIKE	2.68	1.50	0	2.60	0	1	0	0	0	3	-117.7	31.0	0.0%
DIVALIKE	0.16	0.00	0.10	2.61	0	1	0	0	0	4	-109.3	17.1	0.0%
DIVALIKE	2.35	0.90	0	4.38	1.11	1	0	0.91	0	5	-115.3	32.2	0.0%
DIVALIKE	0.24	0.00	0.49	5.49	1.49	1	0	0.62	0	6	-104.1	13.2	0.1%
DIVALIKE	2.56	1.45	0	2.70	0	1	0	0.58	0	4	-117.7	33.8	0.0%
DIVALIKE	0.17	1E-12	0.64	2.81	0	1	0	0.87	0	5	-109.3	20.1	0.0%
BAYAREALIKE	6.40	3.70	0	4.13	2.37	1	0	0	0	4	-129.7	57.8	0.0%
BAYAREALIKE	5.34	3.70	0.95	4.14	2.38	1	0	0	0	5	-122.3	46.2	0.0%
BAYAREALIKE	3.32	3.91	0	2.67	0	1	0	0	0	3	-130.8	57.2	0.0%
BAYAREALIKE	3.34	3.91	0.78	2.67	0	1	0	0	0	4	-123.0	44.4	0.0%
BAYAREALIKE	4.36	3.46	0	5.66	2.45	1	0	0.98	0	5	-129.9	61.4	0.0%
BAYAREALIKE	0.09	0.16	0.35	9.24	3.01	1	0	0.42	0	6	-97.51	0.0	96.5%
BAYAREALIKE	3.36	2.66	0	2.61	0	1	0	0.00	0	4	-132.5	63.5	0.0%
BAYAREALIKE	0.07	1E-12	0.14	2.59	0	1	0	0.14	0	5	-103.4	8.4	1.5%

Results: Model choice

Base model	rate of range expansion *d*	rate of range loss *e*	weight of founder-event speciation *j*	rate of flight -> flightlessness t_{12}	rate of flightlessness -> flight t_{21}	dispersal multiplier when trait=1 (flight) m_1	dispersal multiplier when trait=2 (flightless) m_2	rate of switch to flightlessness during founder event jt_{12}	rate of switch to flight during founder event jt_{21}	number of free parameters np	log-likelihood LnL	delta AICc dAICc	model weight mw
	Black: free parameter that is estimated. Gray: fixed parameter.												
DEC	3.84	1.94	0	3.31	0.94	1	0	0	0	4	-119.6	37.6	0.0%
DEC	0.18	0.00	0.28	5.18	1.65	1	0	0	0	5	-103.9	9.4	0.9%
DEC	3.81	2.01	0	2.58	0	1	0	0	0	3	-120.3	36.2	0.0%
DEC	0.15	0.00	0.16	2.84	0	1	0	0	0	4	-107.5	13.5	0.1%
DEC	2.50	1.69	0	3.60	1.28	1	0	1.00	0	5	-119.4	40.3	0.0%
DEC	0.18	0.00	0.82	4.37	1.12	1	0	0.75	0	6	-104.2	13.3	0.1%
DEC	3.31	1.98	0	2.57	0	1	0	1.00	0	4	-120.2	38.9	0.0%
DEC	0.15	1E-12	0.16	2.84	0	1	0	0.00	0	5	-107.5	16.6	0.0%
DIVALIKE	1.99	0.82	0	5.16	1.48	1	0	0	0	4	-115.2	28.9	0.0%
DIVALIKE	0.24	0.00	0.22	5.73	1.71	1	0	0	0	5	-104.1	9.8	0.7%
DIVALIKE	2.68	1.50	0	2.60	0	1	0	0	0	3	-117.7	31.0	0.0%
DIVALIKE	0.16	0.00	0.10	2.61	0	1	0	0	0	4	-109.3	17.1	0.0%
DIVALIKE	2.35	0.90	0	4.38	1.11	1	0	0.91	0	5	-115.3	32.2	0.0%
DIVALIKE	0.24	0.00	0.49	5.49	1.49	1	0	0.62	0	6	-104.1	13.2	0.1%
DIVALIKE	2.56	1.45	0	2.70	0	1	0	0.58	0	4	-117.7	33.8	0.0%
DIVALIKE	0.17	1E-12	0.64	2.81	0	1	0	0.87	0	5	-109.3	20.1	0.0%
BAYAREALIKE	6.40	3.70	0	4.13	2.37	1	0	0	0	4	-129.7	57.8	0.0%
BAYAREALIKE	5.34	3.70	0.95	4.14	2.38	1	0	0	0	5	-122.3	46.2	0.0%
BAYAREALIKE	3.32	3.91	0	2.67	0	1	0	0	0	3	-130.8	57.2	0.0%
BAYAREALIKE	3.34	3.91	0.78	2.67	0	1	0	0	0	4	-123.0	44.4	0.0%
BAYAREALIKE	4.36	3.46	0	5.66	2.45	1	0	0.98	0	5	-129.9	61.4	0.0%
BAYAREALIKE	0.09	0.16	0.35	9.24	3.01	1	0	0.42	0	6	-97.51	0.0	96.5%
BAYAREALIKE	3.36	2.66	0	2.61	0	1	0	0.00	0	4	-132.5	63.5	0.0%
BAYAREALIKE	0.07	1E-12	0.14	2.59	0	1	0	0.14	0	5	-103.4	8.4	1.5%

Base model		
BAYAREALIKE		
d	rate of range expansion	0.09
e	rate of range loss	0.16
j	weight of founder-event speciation	0.35
t_{12}	rate of flight -> flightlessness	9.24
t_{21}	rate of flightlessness -> flight	3.01
m_1	dispersal multiplier when trait=1 (flight)	1
m_2	dispersal multiplier when trait=2 (flightless)	0
jt_{12}	rate of switch to flightlessness during founder event	0.42
jt_{21}	rate of switch to flight during founder event	0
np	number of free parameters	6
LnL	log-likelihood	-97.51
dAICc	delta AICc	0.0
mw	model weight	96.5%

Results: Model choice

Base model	rate of range expansion *d*	rate of range loss *e*	weight of founder-event speciation *j*	rate of flight -> flightlessness t_{12}	rate of flightlessness -> flight t_{21}	dispersal multiplier when trait=1 (flight) m_1	dispersal multiplier when trait=2 (flightless) m_2	rate of switch to flightlessness during founder event jt_{12}	rate of switch to flight during founder event jt_{21}	number of free parameters np	log-likelihood LnL	delta AICc dAICc	model weight mw
	Black: free parameter that is estimated. Gray: fixed parameter.												
DEC	3.84	1.94	0	3.31	0.94	1	0	0	0	4	-119.6	37.6	0.0%
DEC	0.18	0.00	0.28	5.18	1.65	1	0	0	0	5	-103.9	9.4	0.9%
DEC	3.81	2.01	0	2.58	0	1	0	0	0	3	-120.3	36.2	0.0%
DEC	0.15	0.00	0.16	2.84	0	1	0	0	0	4	-107.5	13.5	0.1%
DEC	2.50	1.69	0	3.60	1.28	1	0	1.00	0	5	-119.4	40.3	0.0%
DEC	0.18	0.00	0.82	4.37	1.12	1	0	0.75	0	6	-104.2	13.3	0.1%
DEC	3.31	1.98	0	2.57	0	1	0	1.00	0	4	-120.2	38.9	0.0%
DEC	0.15	1E-12	0.16	2.84	0	1	0	0.00	0	5	-107.5	16.6	0.0%
DIVALIKE	1.99	0.82	0	5.16	1.48	1	0	0	0	4	-115.2	28.9	0.0%
DIVALIKE	0.24	0.00	0.22	5.73	1.71	1	0	0	0	5	-104.1	9.8	0.7%
DIVALIKE	2.68	1.50	0	2.60	0	1	0	0	0	3	-117.7	31.0	0.0%
DIVALIKE	0.16	0.00	0.10	2.61	0	1	0	0	0	4	-109.3	17.1	0.0%
DIVALIKE	2.35	0.90	0	4.38	1.11	1	0	0.91	0	5	-115.3	32.2	0.0%
DIVALIKE	0.24	0.00	0.49	5.49	1.49	1	0	0.62	0	6	-104.1	13.2	0.1%
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BAYAREALIKE	6.40	3.70	0	4.13	2.37	1	0	0	0	4	-129.7	57.8	0.0%
BAYAREALIKE	5.34	3.70	0.95	4.14	2.38	1	0	0	0	5	-122.3	46.2	0.0%
BAYAREALIKE	3.32	3.91	0	2.67	0	1	0	0	0	3	-130.8	57.2	0.0%
BAYAREALIKE	3.34	3.91	0.78	2.67	0	1	0	0	0	4	-123.0	44.4	0.0%
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BAYAREALIKE	0.07	1E-12	0.14	2.59	0	1	0	0.14	0	5	-103.4	8.4	1.5%

Results: Model choice

Base model matters too!

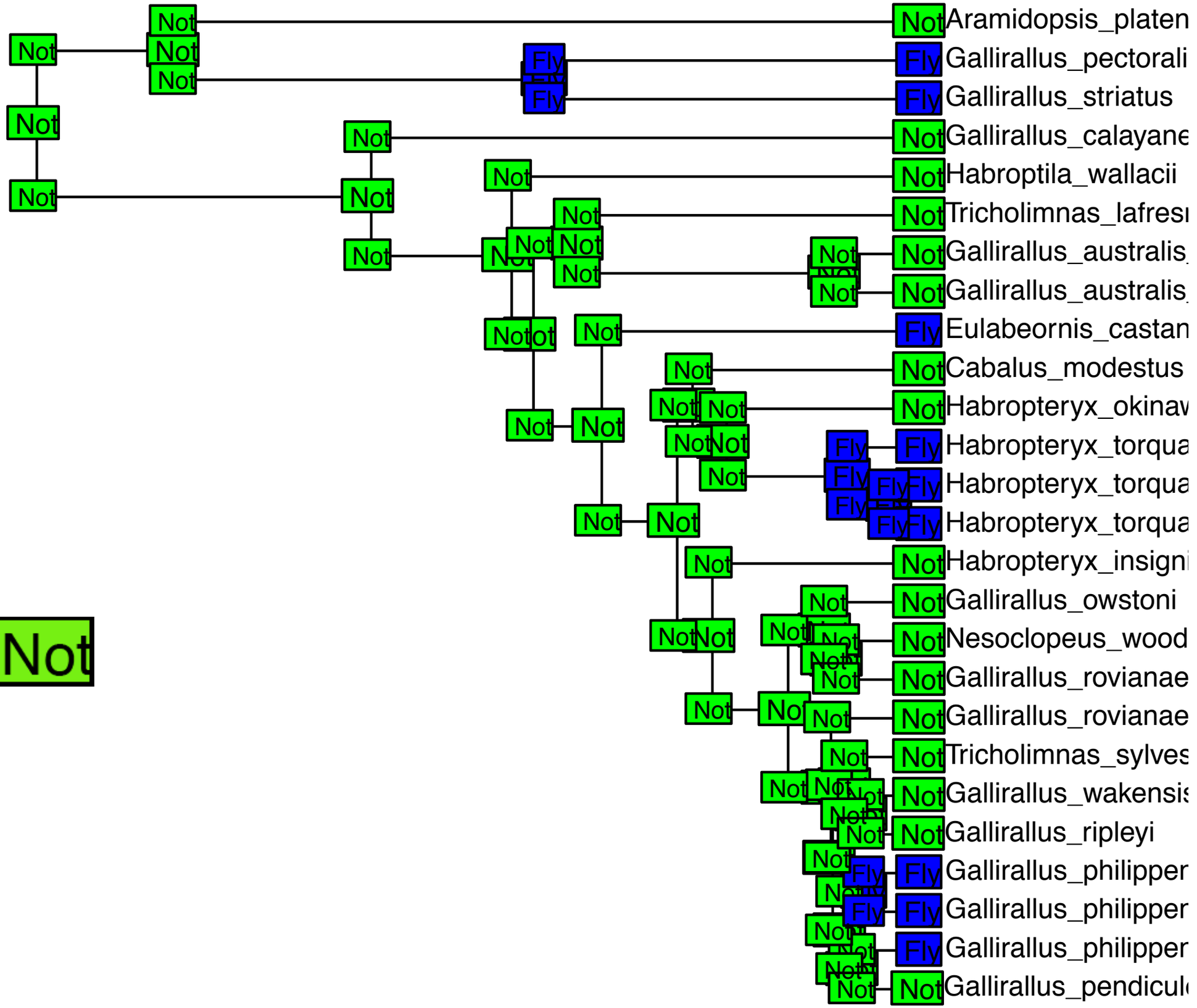
Base model	rate of range expansion *d*	rate of range loss *e*	weight of founder-event speciation *j*	rate of flight -> flightlessness t_{12}	rate of flightlessness -> flight t_{21}	dispersal multiplier when trait=1 (flight) m_1	dispersal multiplier when trait=2 (flightless) m_2	rate of switch to flightlessness during founder event jt_{12}	rate of switch to flight during founder event jt_{21}	number of free parameters np	log-likelihood LnL	delta AICc dAICc	model weight mw
	Black: free parameter that is estimated. Gray: fixed parameter.												
DEC	3.84	1.94	0	3.31	0.94	1	0	0	0	4	-119.6	37.6	0.0%
DEC	0.18	0.00	0.28	5.18	1.65	1	0	0	0	5	-103.9	9.4	0.9%
DEC	3.81	2.01	0	2.58	0	1	0	0	0	3	-120.3	36.2	0.0%
DEC	0.15	0.00	0.16	2.84	0	1	0	0	0	4	-107.5	13.5	0.1%
DEC	2.50	1.69	0	3.60	1.28	1	0	1.00	0	5	-119.4	40.3	0.0%
DEC	0.18	0.00	0.82	4.37	1.12	1	0	0.75	0	6	-104.2	13.3	0.1%
DEC	3.31	1.98	0	2.57	0	1	0	1.00	0	4	-120.2	38.9	0.0%
DEC	0.15	1E-12	0.16	2.84	0	1	0	0.00	0	5	-107.5	16.6	0.0%
DIVALIKE	1.99	0.82	0	5.16	1.48	1	0	0	0	4	-115.2	28.9	0.0%
DIVALIKE	0.24	0.00	0.22	5.73	1.71	1	0	0	0	5	-104.1	9.8	0.7%
DIVALIKE	2.68	1.50	0	2.60	0	1	0	0	0	3	-117.7	31.0	0.0%
DIVALIKE	0.16	0.00	0.10	2.61	0	1	0	0	0	4	-109.3	17.1	0.0%
DIVALIKE	2.35	0.90	0	4.38	1.11	1	0	0.91	0	5	-115.3	32.2	0.0%
DIVALIKE	0.24	0.00	0.49	5.49	1.49	1	0	0.62	0	6	-104.1	13.2	0.1%
DIVALIKE	2.56	1.45	0	2.70	0	1	0	0.58	0	4	-117.7	33.8	0.0%
DIVALIKE	0.17	1E-12	0.64	2.81	0	1	0	0.87	0	5	-109.3	20.1	0.0%
BAYAREALIKE	6.40	3.70	0	4.13	2.37	1	0	0	0	4	-129.7	57.8	0.0%
BAYAREALIKE	5.34	3.70	0.95	4.14	2.38	1	0	0	0	5	-122.3	46.2	0.0%
BAYAREALIKE	3.32	3.91	0	2.67	0	1	0	0	0	3	-130.8	57.2	0.0%
BAYAREALIKE	3.34	3.91	0.78	2.67	0	1	0	0	0	4	-123.0	44.4	0.0%
BAYAREALIKE	4.36	3.46	0	5.66	2.45	1	0	0.98	0	5	-129.9	61.4	0.0%
BAYAREALIKE	0.09	0.16	0.35	9.24	3.01	1	0	0.42	0	6	-97.51	0.0	96.5%
BAYAREALIKE	3.36	2.66	0	2.61	0	1	0	0.00	0	4	-132.5	63.5	0.0%
BAYAREALIKE	0.07	1E-12	0.14	2.59	0	1	0	0.14	0	5	-103.4	8.4	1.5%

Distribution of flight in Pacific Rails

(standard trait model)

Flying: Fly

Non-flying: Not



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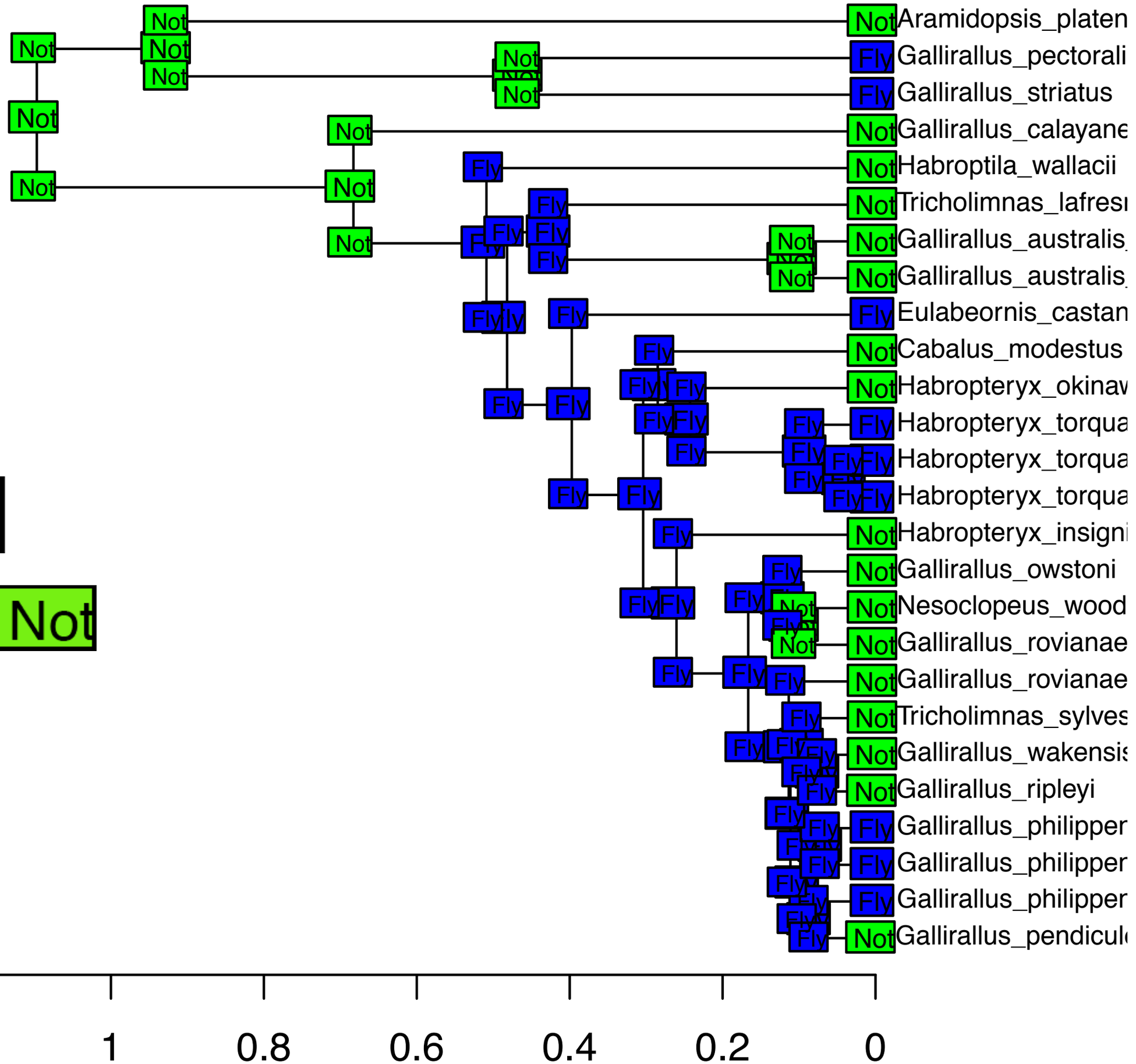
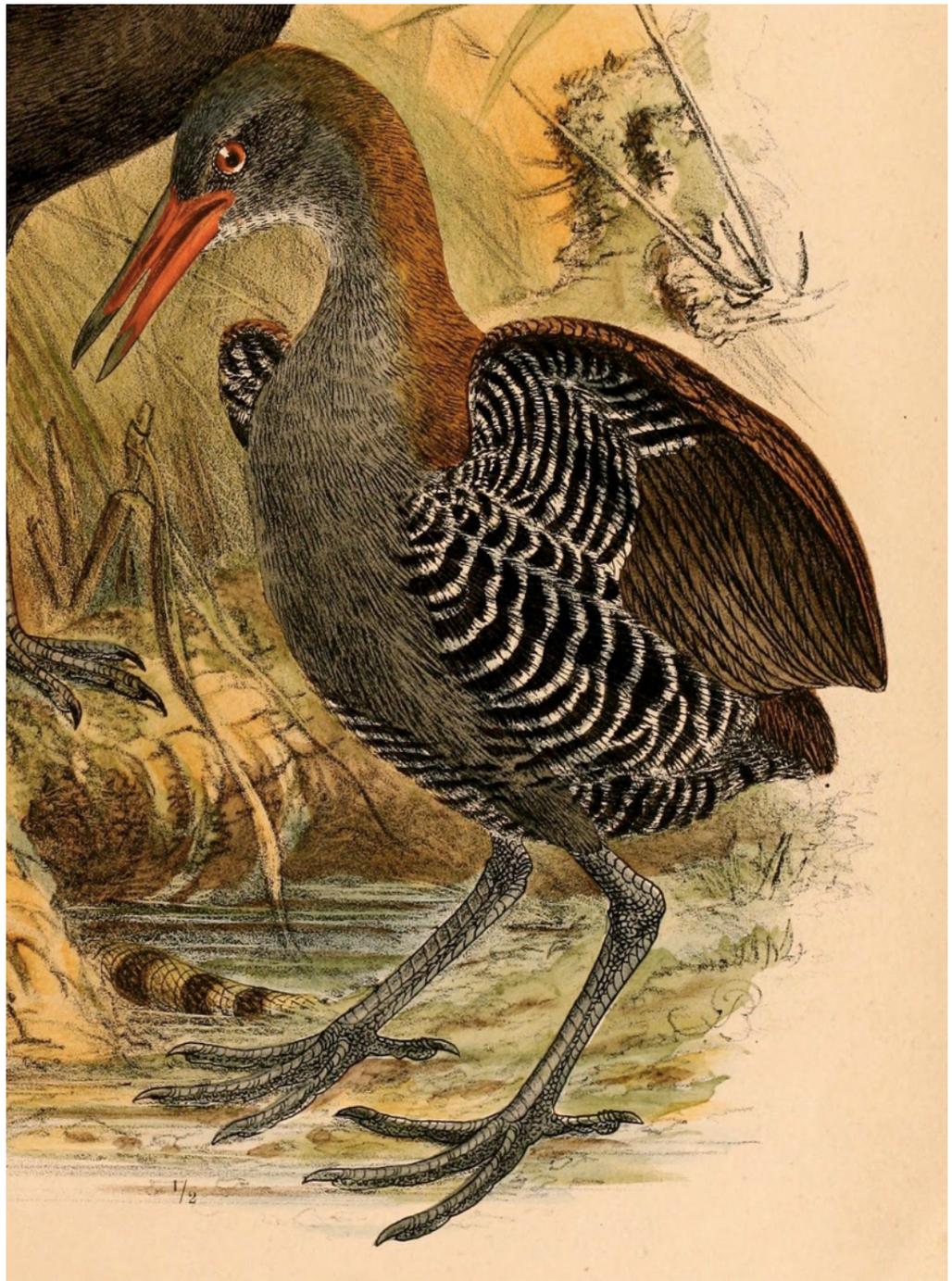




Snoring rail, *Aramidopsis plateni*
(flightless, Sulawesi)

Adolf Meyer (1898), *The Birds of Celebes and the neighbouring islands*. https://en.wikipedia.org/wiki/Snoring_rail

Conclusions

1. Trait-based dispersal models are feasible, at least for moderate-sized problems

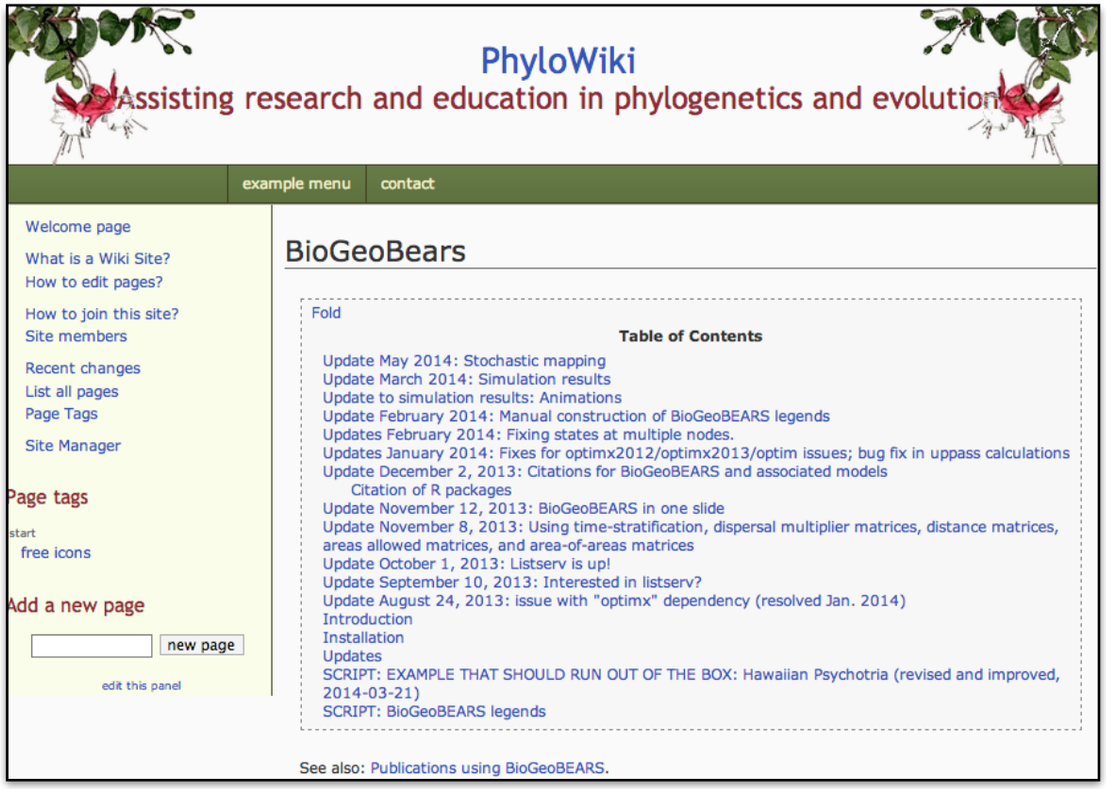
(key issue: size of matrices)

2. Trait evo. & its influence on dispersal can be revealed by parameter *estimation*

3. Combinable with distance, etc.

4. Adding to *BioGeoBEARS*; email me to try it: nick.matzke@anu.edu.au

Thanks! I welcome questions/comments/ collaborations at: nick.matzke@anu.edu.au



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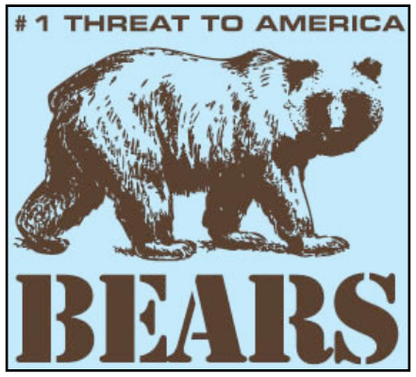
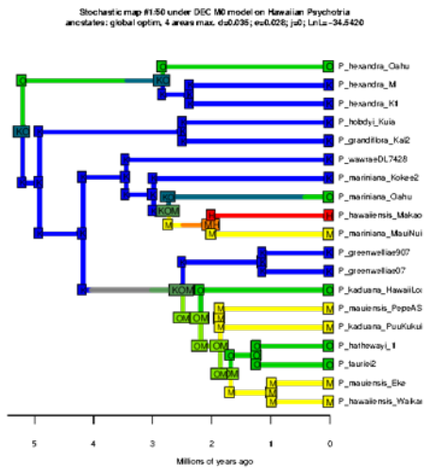
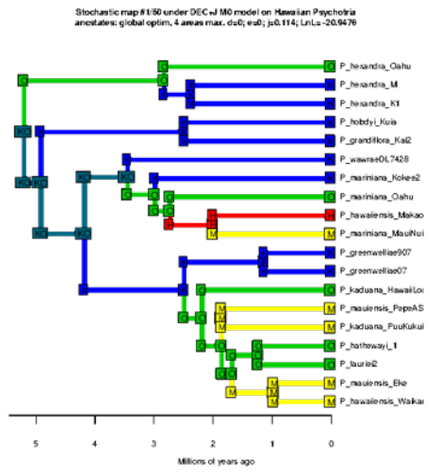


TRY *BIOGEOBEARS* AT:

http://phylo.wikidot.com/biogeobears





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NIMBioS
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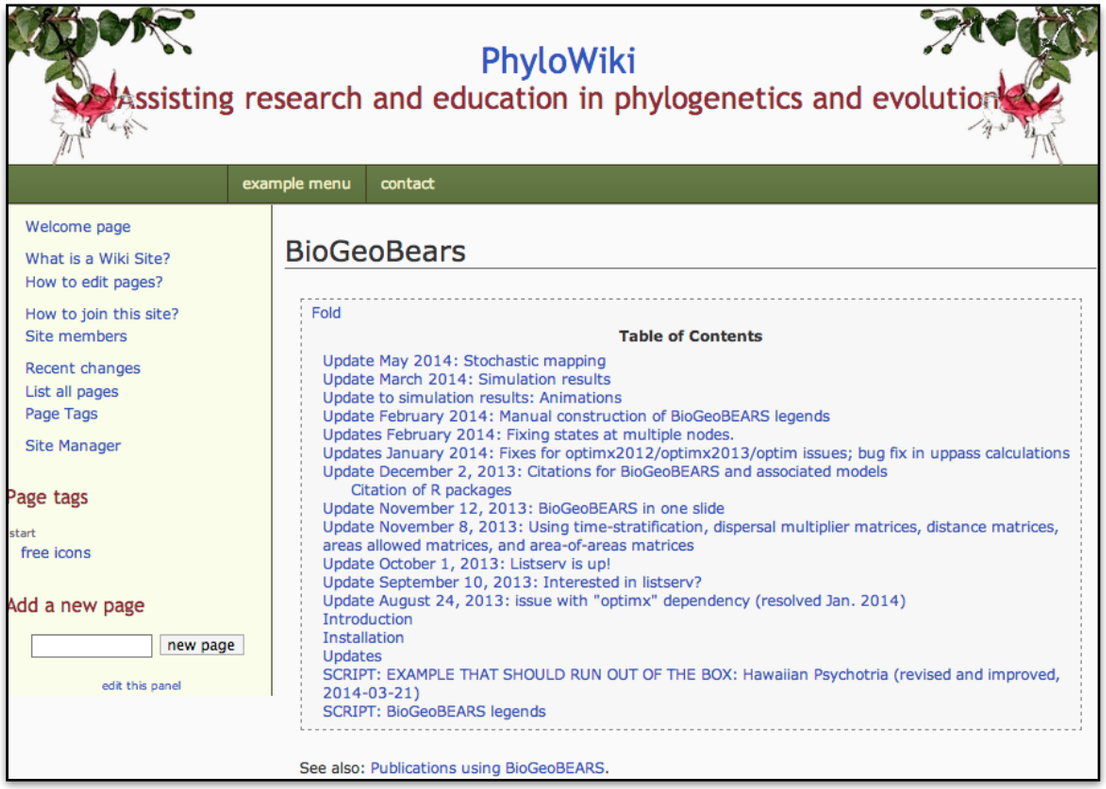
Bachtrog • Eisen • Hallatschek • Huelsenbeck • Nielsen • Slatkin • Song

Thanks! I welcome questions/comments/ collaborations at: nick.matzke@anu.edu.au



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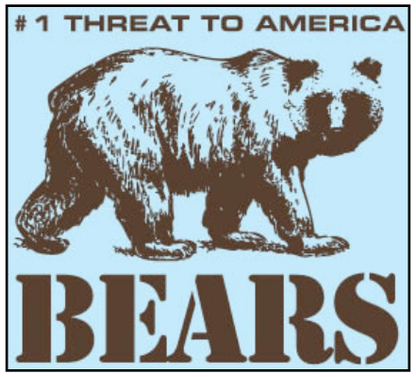

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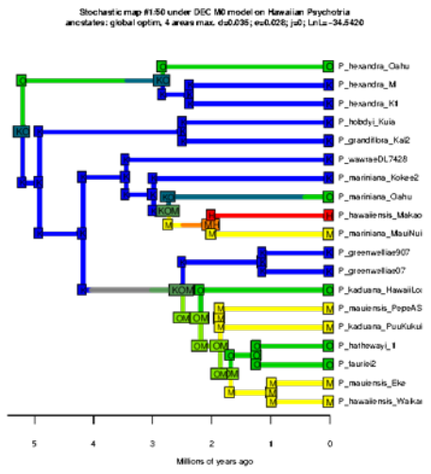

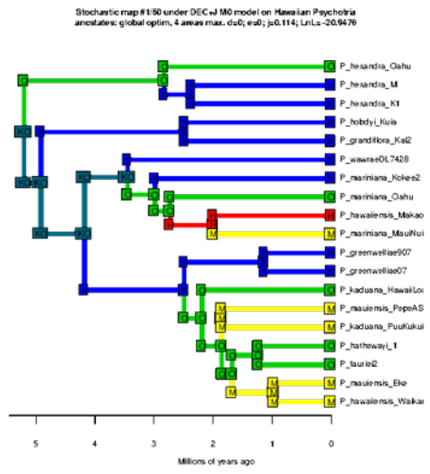

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