

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



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(Data provided by collaborator Jeremy J. Kirchman)

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Twitter and photos are OK!
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QR code: CV, website, R code!

Abstract

Organism traits must be important in historical biogeography. In particular, rates of dispersal (both range-expansion dispersal, and jump dispersal leading to founder-event speciation) must depend to some degree on traits such as flight and its loss, and seed dispersal mechanisms and the dispersal abilities of animals that transport seeds.

However, to date no probabilistic historical biogeographical models have been available that allow geographic range and traits to co-evolve on the phylogeny, with traits influencing dispersal ability. In purely continuous-time Markov models, adding a trait is just a matter of doubling the size of the rate matrix; however, biogeographical models also include a much more complex discrete-time model describing how geographic range can change during cladogenesis. Traits might also influence this process.

I present an addition to the R package *BioGeoBEARS* that enables an evolving discrete trait to influence dispersal ability for both anagenetic and cladogenetic range change. This model can be freely combined with models adding jump dispersal (e.g., DEC+J), distance as a predictor of dispersal (+x models, with dispersal rate multiplied by distance^x), and other variants. I test the model against simulations and datasets where large evolutionary changes in dispersal ability are highly likely (e.g., Pacific rails, which have repeatedly lost flight).

BioGeoBEARS trait + dispersal model

Build a trait-based dispersal model

1. Trait flight/flightlessness trait evolves on tree

Parameters of model:

t_{12} -> Rate of flight loss

t_{21} -> Rate of flight gain

m_2 -> Multiplier on dispersal prob. while flightless

	FLY	NOT
FLY	-	t_{12}
NOT	t_{21}	-

2. Cladogenetic parameters of model:

jt_{12} -> Chance of "jumping" from flight-> flightless during founder-event speciation

Study system: "typical" rails of the Pacific



G. pacificus, from Tahiti, "known only from a painting made by Georg Forster on James Cook's second voyage."

Adolf Meyer (1888). The Birds of Celebes and the neighbouring islands. https://en.wikimedia.org/wiki/File:Shooting_cail

Data from: Kirchman (2012)

Collaborator: Jeremy J. Kirchman, Curator of Birds, New York State Museum

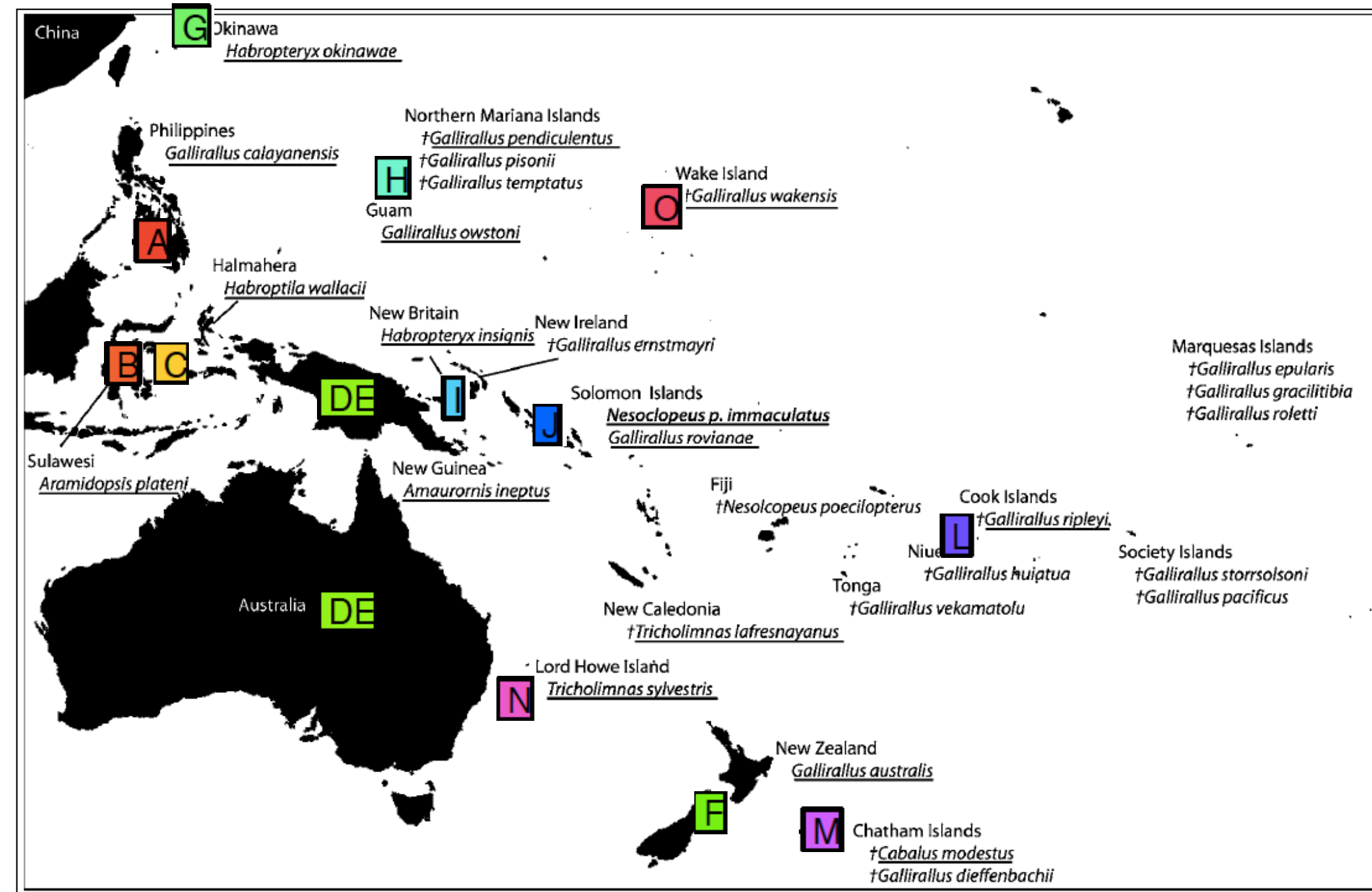


FIG. 1. Map showing the distribution of all known living and extinct (†) flightless species of "typical" rails from Pacific islands. The ranges of the volant Source: Kirchman, Jeremy J. (2012). Speciation of Flightless Rails on Islands: A DNA-Based Phylogeny of the Typical Rails of the Pacific. *The Auk*, 129(1):56-69.

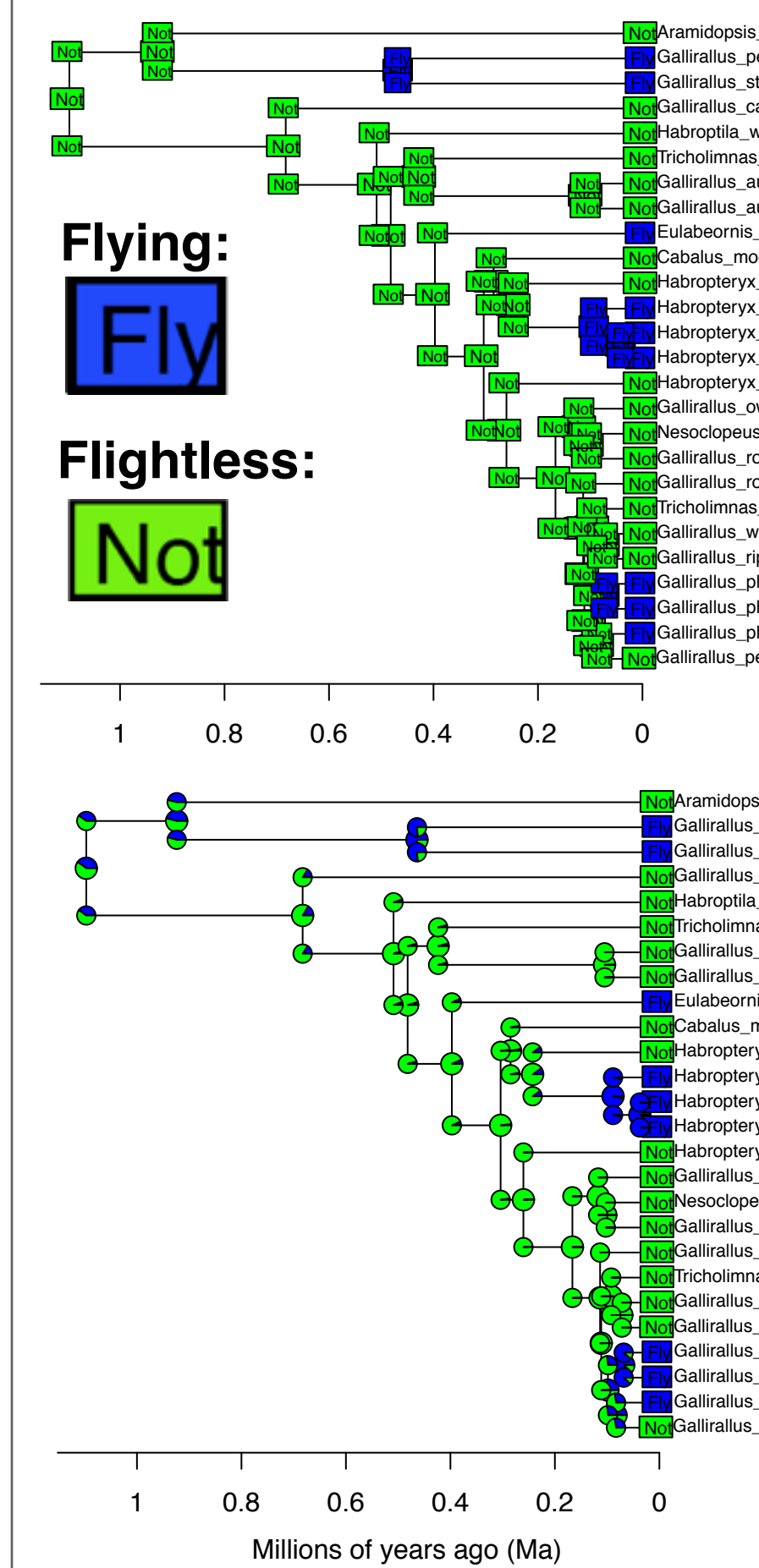
Statistical Model Choice

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

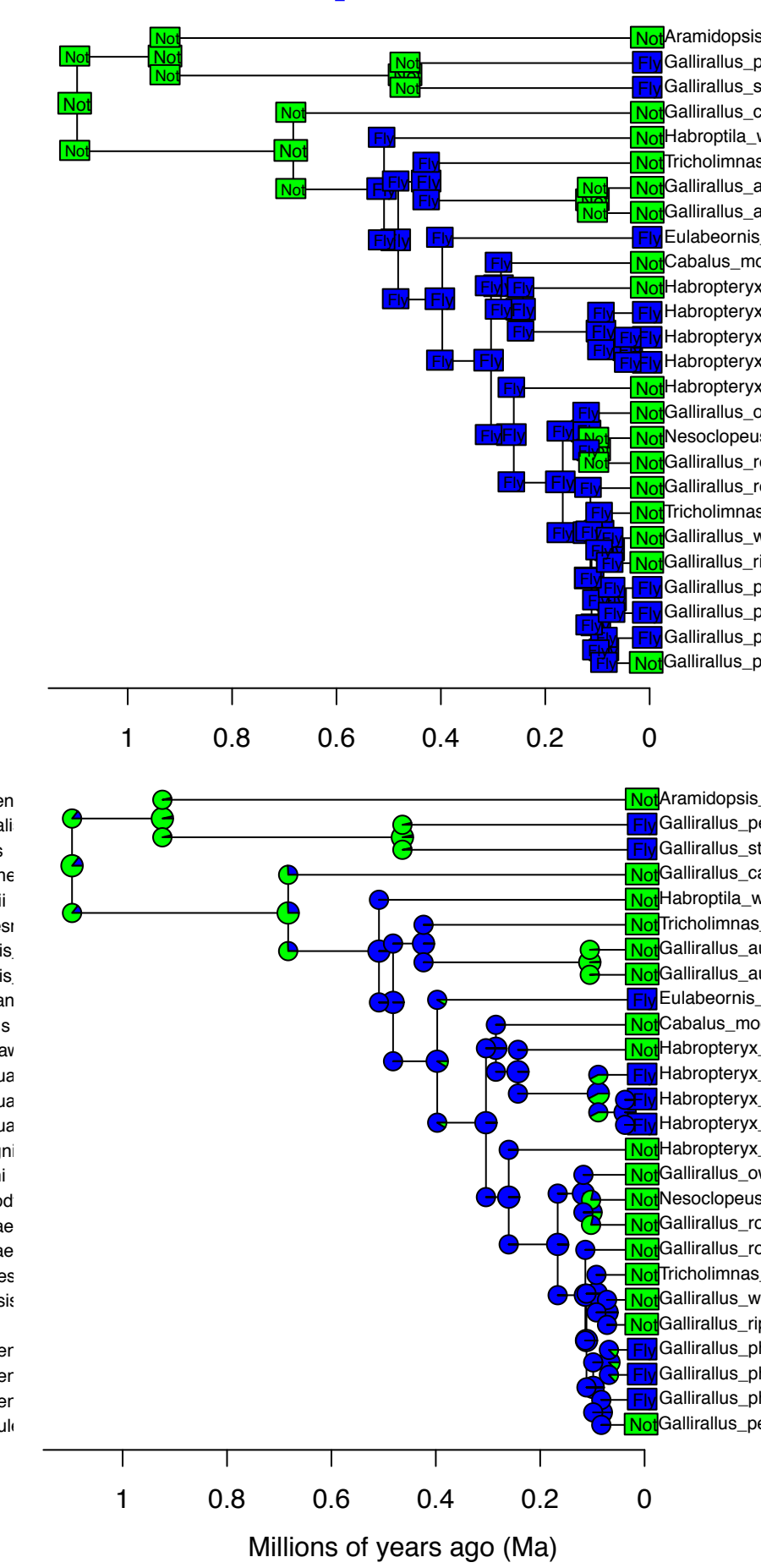
Black: free parameter that is estimated. Gray: fixed parameter.

Best Model under these constraints

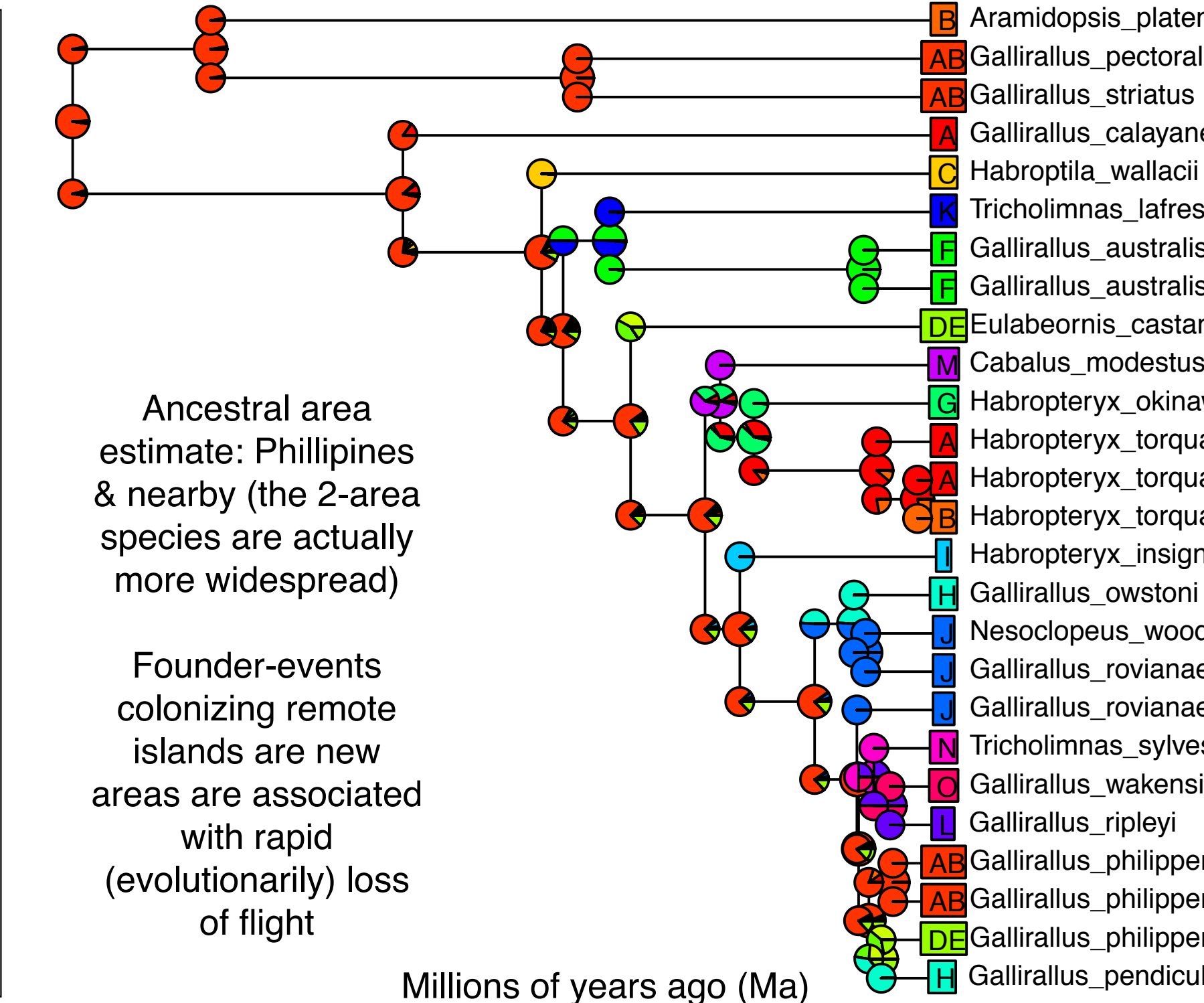
Standard trait model



Trait+dispersal model



Results: Ancestral geography



Ancestral area estimate: Philippines & nearby (the 2-area species are actually more widespread)

Founder-events colonizing remote islands are new areas are associated with rapid (evolutionarily) loss of flight

Millions of years ago (Ma)

Conclusions

Linked trait+dispersal model allows statistical inferences not possible with either individually. Although this case is "obvious," in many datasets, the influence of traits on dispersal may be unknown.

- Flightlessness is more frequent at the tips, so models that allow reversal are favored. Regardless, the trait inference is improved (not perfect, see root).
- Inferring m_2 is difficult, but fixing to 0 is feasible and nearly as good (~1 LnL).
- Founder-event speciation is a key process, as is founder+flight loss.
- The base model matters a lot. This must be part of the model choice!
- These models ignore lineage extinction, but ClaSSE models infeasible.
- Models with more areas will be slower, but *BioGeoBEARS* is parallelized.

Check out *BioGeoBEARS*, updated code at PhyloWiki: <http://phylo.wikidot.com/>