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

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The Australian National University
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phylo.wikidot.com/BioGeoBEARS

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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
<table>
<thead>
<tr>
<th>Process</th>
<th>Ranges Before</th>
<th>After</th>
<th>Character mapping</th>
<th>DIVA (LAGRANGE)</th>
<th>DEC (LAGRANGE)</th>
<th>BayArea, BBM (RASP)</th>
<th>Par Bio/ Su</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dispersal</td>
<td></td>
<td></td>
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<td>✓</td>
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</tr>
<tr>
<td>Extinction</td>
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<td></td>
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<td>✓</td>
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<td>✓</td>
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<tr>
<td>Range-switching</td>
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<tr>
<td>Sympathy (narrow)</td>
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<td></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
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<tr>
<td>Sympathy (widespread)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>✓</td>
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<tr>
<td>Sympathy (subset)</td>
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<td>✓</td>
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<tr>
<td>Vicariance (narrow)</td>
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<td></td>
<td></td>
<td>✓</td>
<td>✓</td>
<td></td>
<td>✓</td>
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<tr>
<td>Vicariance (widespread)</td>
<td></td>
<td></td>
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<td>✓</td>
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<tr>
<td>Founder</td>
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</tr>
</tbody>
</table>

*BioGeoBEARS supermodel can produce various submodels*
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:

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”

Data from:

Jeremy J. Kirchman
Curator of Birds
New York State Museum

Snoring rail, Aramidopsis plateni
(flightless, Sulawesi)

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

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

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.

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

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
Areas (simplified from Kirchman)

- Phillipines
- Sulawesi
- Mollucas
- PNG, Australia
- New Zealand
- Okinawa
- Guam/Marianas
- New Britain
- Solomon Islands
- Cook Islands
- Chatham Islands
- Lord Howe Island
- Wake Island

Dated phylogeny of typical Rails (simplified from Kirchman)

- Aramidopsis plateni
- Gallirallus pectoralis
- Gallirallus striatus
- Gallirallus calayanensis
- Habroptila wallacii
- Tricholimnas lafresnayanus
- Gallirallus australis greyi
- Gallirallus australis australis
- Eulabeornis castaneoventris
- Cabalus modestus
- Habropteryx okinawae
- Habropteryx torquatus torquatus
- Habropteryx torquatus sulcirostris
- Habropteryx torquatus celebensis
- Habropteryx insignis
- Gallirallus owstoni
- Nesoclopeus woodfordi immaculatus
- Gallirallus roviana 826433
- Gallirallus roviana 28014
- Tricholimnas sylvestris 1896
- Gallirallus wakensis
- Gallirallus ripleyi
- Gallirallus philippensis 425075
- Gallirallus philippensis 194032
- Gallirallus philippensis mellori
- Gallirallus pendiculentus
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
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:

- $t_{12}$ -> Rate of flight loss
- $t_{21}$ -> Rate of flight gain
- $m_2$ -> 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:

<table>
<thead>
<tr>
<th></th>
<th>FLY</th>
<th>NOT</th>
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</thead>
<tbody>
<tr>
<td>FLY</td>
<td>-</td>
<td>t12</td>
</tr>
<tr>
<td>NOT</td>
<td>t21</td>
<td>-</td>
</tr>
</tbody>
</table>

$t12 \rightarrow$ Rate of flight loss
$t21 \rightarrow$ Rate of flight gain
$m2 \rightarrow$ 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:

- $t_{12}$ -> Rate of flight loss
- $t_{21}$ -> Rate of flight gain
- $m_2$ -> Multiplier on dispersal prob. while flightless

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:
   \( jt12 \rightarrow \) Chance of “jumping” from flight-\( \rightarrow \)
   flightless during founder-event speciation
Trait-dependent DEC model

Traditional:

Dispersal-Extinction (on branches)

\[ \begin{align*} d & = \text{rate of “dispersal”} \\
& = \text{(range expansion)} \\
e & = \text{rate of “extinction”} \\
& = \text{(range contraction / local extirpation)} \end{align*} \]

Rate matrix:

<table>
<thead>
<tr>
<th>ancestor range</th>
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<th>A</th>
<th>B</th>
<th>AB</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td></td>
<td>e</td>
<td>-</td>
<td>d</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td>e</td>
<td>-</td>
<td>d</td>
</tr>
<tr>
<td>AB</td>
<td>e</td>
<td>e</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
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:

<table>
<thead>
<tr>
<th></th>
<th>null</th>
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<th>B</th>
<th>AB</th>
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<tbody>
<tr>
<td><strong>null</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><strong>A</strong></td>
<td>( e )</td>
<td>-</td>
<td>-</td>
<td>( d )</td>
</tr>
<tr>
<td><strong>B</strong></td>
<td>( e )</td>
<td>-</td>
<td>-</td>
<td>( d )</td>
</tr>
<tr>
<td><strong>AB</strong></td>
<td>( e )</td>
<td>( e )</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Trait-dependent:

Rate matrix:
Trait-dependent DEC model

Traditional:

Dispersal-Extinction (on branches)

\[ d = \text{rate of "dispersal" (range expansion)} \]
\[ e = \text{rate of "extinction" (range contraction / local extirpation)} \]

Rate matrix:

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<thead>
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<th></th>
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</thead>
<tbody>
<tr>
<td>FLY</td>
<td>-</td>
<td>t12</td>
</tr>
<tr>
<td>NOT</td>
<td>t21</td>
<td>-</td>
</tr>
</tbody>
</table>

Trait-dependent:

Rate matrix:

\[
\begin{array}{ccc}
\text{null} & A & B & AB \\
\text{null} & - & & \\
A & e & - & d \\
B & e & - & d \\
AB & e & e & - \\
\end{array}
\]
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:

<table>
<thead>
<tr>
<th></th>
<th>null</th>
<th>A</th>
<th>B</th>
<th>AB</th>
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</thead>
<tbody>
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<td>-</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>$e$</td>
<td>-</td>
<td>$d$</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>$e$</td>
<td>-</td>
<td>$d$</td>
</tr>
<tr>
<td></td>
<td>AB</td>
<td>$e$</td>
<td>$e$</td>
<td>-</td>
</tr>
</tbody>
</table>

**Trait-dependent:**

Rate matrix:

<table>
<thead>
<tr>
<th></th>
<th>FLY</th>
<th>NOT</th>
</tr>
</thead>
<tbody>
<tr>
<td>FLY</td>
<td>-</td>
<td>$t_{12}$</td>
</tr>
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<td>$t_{21}$</td>
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<table>
<thead>
<tr>
<th></th>
<th>null</th>
<th>A</th>
<th>B</th>
<th>AB</th>
</tr>
</thead>
<tbody>
<tr>
<td>ancestor</td>
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<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>$e$</td>
<td>-</td>
<td>$d$</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>$e$</td>
<td>-</td>
<td>$d$</td>
</tr>
<tr>
<td></td>
<td>AB</td>
<td>$e$</td>
<td>$e$</td>
<td>-</td>
</tr>
</tbody>
</table>
trait matrix + dispersal/extinction

\[
\begin{array}{|c|c|}
\hline
FLY & NOT \\
\hline
FLY & - & t12 \\
\hline
NOT & t21 & - \\
\hline
\end{array}
\]

\[
\begin{array}{|c|c|c|c|}
\hline
null & A & B & AB \\
\hline
null & - & & \\
A & e & - & d \\
B & e & - & d \\
AB & e & e & - \\
\hline
\end{array}
\]

=
trait matrix + dispersal/extinction

<table>
<thead>
<tr>
<th></th>
<th>FLY</th>
<th>NOT</th>
</tr>
</thead>
<tbody>
<tr>
<td>FLY</td>
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<td>t12</td>
</tr>
<tr>
<td>NOT</td>
<td>t21</td>
<td>-</td>
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</tbody>
</table>

\[ + \]

ancestor range

<table>
<thead>
<tr>
<th></th>
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<th>B</th>
<th>AB</th>
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<tr>
<td>null</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>e</td>
<td>-</td>
<td>d</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>e</td>
<td>-</td>
<td>d</td>
<td></td>
</tr>
<tr>
<td>AB</td>
<td>e</td>
<td>e</td>
<td>-</td>
<td></td>
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</tbody>
</table>

descendant range

<table>
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<th>B</th>
<th>AB</th>
</tr>
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</tr>
<tr>
<td>A</td>
<td>e</td>
<td>-</td>
<td>d</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>e</td>
<td>-</td>
<td>d</td>
<td></td>
</tr>
<tr>
<td>AB</td>
<td>e</td>
<td>e</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

Combined anagenetic matrix

\[ + \]

\[ t12 \]

\[ t21 \]
DEC+J model: add trait to jump
(Matzke 2014)

Traditional:

Cladogenesis
(at splits)

Equal per-event weights
(modified by \( j \) in DEC+J)

Jump dispersal (founder events)

Sympatry (narrow)

Sympatry (subset)

Vicariance (narrow)
DEC+J model: add trait to jump
(Matzke 2014)

Traditional:

Cladogenesis
(at splits)

Equal per-event weights
(modified by $j$ in DEC+J)

Jump dispersal
(founder events)

Sympathy (narrow)

Sympathy (subset)

Vicariance (narrow)

Trait-dependent:

Cladogenesis
(at splits)
DEC+J model: add trait to jump (Matzke 2014)

**Traditional:**

**Cladogenesis (at splits)**

- **Equal per-event weights**
  - (modified by $j$ in DEC+J)
- **Jump dispersal (founder events)**

**Sympatry (narrow)**

**Sympatry (subset)**

**Vicariance (narrow)**

**Trait-dependent:**

**Cladogenesis (at splits)**

- **Founder**
DEC+J model: add trait to jump
(Matzke 2014)

Traditional:

Cladogenesis
(at splits)

Equal per-event weights
(modified by $j$ in DEC+J)

Jump dispersal (founder events)

Sympatry (narrow)

Sympatry (subset)

Vicariance (narrow)

Trait-dependent:

Cladogenesis
(at splits)

Trait model:
DEC+J model: add trait to jump (Matzke 2014)

Traditional:

Cladogenesis (at splits)

Equal per-event weights
(modified by j in DEC+J)

Jump dispersal (founder events)

Sympathy (narrow)

Sympathy (subset)

Vicariance (narrow)

Trait model:

Traditional: Trait-dependent:

Cladogenesis (at splits)

Founder

Trait model:

m2 x

Founder
Cladogenetic range-change model: DEC

Cladogenetic range-change events:

- **Sympatry** (narrow)
- **Sympatry** (subset)
- **Vicariance** (narrow)

Cladogenetic transition matrix:

```
  A  B  C  AB  BC  AC  ABC
left:  sym  sym  sym
      vic  vic  vic
      vic  vic  vic
      vic  vic  vic

  A  B  C  AB  BC  AC  ABC
right: sym  sym  sym
      vic  vic  vic
      vic  vic  vic
      vic  vic  vic

  count: 1  1  6  6  6  12
```
Cladogenetic range-change model: DEC+J

Cladogenetic range-change events:

Cladogenetic transition matrix:
Trait-based cladogenetic model: DEC+J

Cladogenetic range-change events:

Cladogenetic transition matrix while flying:

Cladogenetic transition matrix while non-flying: $j = m \times j$
## Results: Model choice

<table>
<thead>
<tr>
<th>Base model</th>
<th>$d$</th>
<th>$e$</th>
<th>$j$</th>
<th>$t_{12}$</th>
<th>$t_{21}$</th>
<th>$m_1$</th>
<th>$m_2$</th>
<th>$jt_{12}$</th>
<th>$jt_{21}$</th>
<th>np</th>
<th>LnL</th>
<th>dAICc</th>
<th>model weight</th>
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<tbody>
<tr>
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<td>0.94</td>
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<td>0</td>
<td>0</td>
<td>4</td>
<td>-119.6</td>
<td>37.6</td>
<td>0.0%</td>
</tr>
<tr>
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<td>0.18</td>
<td>0.00</td>
<td>0.28</td>
<td>5.18</td>
<td>1.65</td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>-120.3</td>
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<td>1</td>
<td>0</td>
<td>0</td>
<td>1.00</td>
<td>0</td>
<td>-107.5</td>
<td>13.5</td>
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<td>5</td>
<td>-107.5</td>
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<tr>
<td>DIVALIKE</td>
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<td>9.8</td>
<td>0.7%</td>
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### Results: Model choice

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## Results: Model choice

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</table>

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

Base model matters too!
Distribution of flight in Pacific Rails (standard trait model)

Flying: Fly

Non-flying: Not
Distribution of flight in Pacific Rails (standard trait model)

Flying: Fly
Non-flying: Not
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

Thanks especially to:

Jeremy Kirchman
Craig Moritz
ANU
ARC DECRA

NIMBioS
Brian O’Meara
Jeremy Beaulieu
Katie Massana
Michael Landis

TRY BIOGEOBEARS AT: http://phylo.wikidot.com/biogeobears

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UC Berkeley Wang Fellowship
UC Berkeley Tien Fellowship
Google Summer of Code
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