Putting Evolution Into Ecological Niche Modelling
(And: Statistical model choice in phylogenetic biogeography more generally)

*BioGeoBEARS* inference of dispersal events for 14,000 plant species

**Figure:** Dispersal events between ecoregion centroids, 0.1-1 Ma.

**Method:** Biogeographical stochastic mapping

**Model:** BAYAREALIKE+a+distance+environmental distance

**Software:** *BioGeoBEARS* (Matzke 2013-2015)

**Data:** Angiosperm megaphylogeny
(14,000 species from Zanne *et al.* 2013)

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Thanks for support from:

![Sponsors logos]

**Nicholas J. Matzke**

DECRA Fellow

Division of Ecology, Evolution, and Genetics
Research School of Biology
The Australian National University


Talk details: November 16, 2015, 12 noon
Mathematics & Physics, University of Tasmania
Tweeted to #SMMP2015
Tweeted to #SMMP2015
Nicholas J. Matzke

At the Stochastic Modelling Meets Phylogenetics Meeting at U. Tasmania! http://www.maths.utas.edu.au/Peo.../oreilly/SMMP/smpp2015.html ...
#SMMP2015 Logo=WIN!

Nick Matzke on Twitter

“At the Stochastic Modelling Meets Phylogenetics Meeting at U. Tasmania! https://t.co/cgqq2OR5MO
#SMMP2015 Logo=WIN!”

T. Ryan Gregory
Hi, I'm Lefty, the left-handed DNA cartoon!

Nicholas J. Matzke
I believe the organizer's artist son made the graphic 😞

T. Ryan Gregory
Well you tell that kid he got it backwards. NO MERCY.
Statistical model choice in phylogenetic biogeography

Biogeography:
The geography of life
Statistical model choice in phylogenetic biogeography

Biogeography:
The geography of life
Statistical model choice in phylogenetic biogeography

Biogeography:
The geography of life

Ecological biogeography

Historical biogeography
Statistical model choice in phylogenetic biogeography

Biogeography: The geography of life

Ecological biogeography
- Focus: Environmental controls on distribution
- Ecological interactions
- Timescale: the Recent

Historical biogeography
Biogeography: The geography of life

**Ecological biogeography**
- Focus: Environmental controls on distribution
- Ecological interactions
- Timescale: the Recent

**Historical biogeography**
- Focus: Evolutionary history of distributions
- Dispersal/vicariance events
- Timescale: Millions of years
Biogeography: The geography of life

**Ecological biogeography**
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**Historical biogeography**
- Focus: Evolutionary history of distributions
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- Timescale: Millions of years
- 2000s: PHYLOGENIES
Statistical model choice in phylogenetic biogeography

Biogeography: The geography of life

What is historical biogeography good for?

Charles Lyell:

“The present is the key to the past.”

Flip it around:

“The past is the key to the present.”

Lithograph of Charles Lyell made in Philadelphia by J. E. Mayall during Lyell’s visit to America in the 1840s.
Figure 2. Growth in phylogenetics studies. By 2013, studies involving phylogenies were ~1% of all published science (David Hillis, pers. comm.). Data: Scopus, 9/2014.
Statistical model choice in phylogenetic biogeography

Outline:
1. Introduction
2.
3.
1.
I think we should use statistical model choice in biogeography

Requirements for statistical model choice:

1. Multiple models that calculate the likelihood of the data

2. Maximum likelihood (ML) optimizer (or Bayesian MCMC)
I think we should use statistical model choice in biogeography

Model choice already ubiquitous:

- DNA model choice in phylogenetics (JC69 vs. HKY vs. GTR, etc.)

- Trait evolution on phylogenies (e.g. Brownian vs. O-U process, e.g. Hunt 2007)

- Paleobiology (e.g. Foote 2012)


Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
   Founder-event speciation
   Geographic distance
   Environmental distance
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, and island biogeography.
- However, so far ignored in historical biogeography models.
Extreme case: tortoise dispersal

Gerlach et al. (2006), Tortoise Oceanic Dispersal
A short, biased history of Historical Biogeography
Dispersal versus Vicariance

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).
Plate tectonics led many to favor vicariance.

Alan de Queiroz on the vicariance biogeography paradigm:

“Donoghue also thinks, as do many other biogeographers, that the vicariance people are crazy to ignore the molecular dating evidence. He sees their dismissal of this evidence as ‘misguided’ and a case of ‘burying their heads in the sand.’” (p. 135)
Review by Malte Ebach:

The timely arrival of *Tewkesbury Walks* acts as an antidote to the extreme reactionary neo-dispersalism of, for example, the recently published *The Monkey's Journey* (de Queiroz 2014).

The latter book contends that some cladists foolishly reject dispersal outright. I do not think this is true. These cladists are emphasizing that dispersal is immune to discovery, rather than refuting its existence.


(bold added)

For more, see:


Each method makes assumptions

Methods in use include:

• Biogeography as a standard character (parsimony, likelihood, Bayesian)

• DIVA (Dispersal-Vicariance Analysis) (parsimony) Ronquist 1997

• Lagrange-DEC (Dispersal-Extinction-Cladogenesis) (likelihood) Ree & Smith 2008

• RASP-BBM: Bayesian Binary Model (also, RASP does DIVA, DEC)

• BayArea (Bayesian) Landis, Matzke et al. 2013
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**Anagenetic**

- Sympathy (narrow)
- Sympathy (widespread)
- Sympathy (subset)

**Cladogenetic**

- Vicariance (narrow)
- Vicariance (widespread)
- Founder
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Figure 1, Matzke 2013, *Frontiers of Biogeography*
Which model should we use?

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Which model should we use?

What about founder-event speciation?
I think we should use statistical model choice in biogeography.
I think we should use statistical model choice in biogeography.

What about founder-event speciation?
Standard model: “Dispersal-Extinction Cladogensis” (DEC)

Published in Ree & Smith (2008), Sys. Bio.; Used in 500+ publications

Cladogenetic range-change events:

Cladogenetic transition matrix:
Cladogenetic range-change events:

Sympathy (narrow)

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Founder-event speciation

Cladogenetic transition matrix:

Modified model: DEC+J

Published in Matzke (2014), Sys. Bio.; Used in 50+ publications
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Before | After | DEC (LAGRANGE)
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Ranges

Before

After

DEC (LAGRANGE)

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Ranges

Before

After

DEC (LAGRANGE)

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Before

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DEC

(LAGRANGE)

Per-event weights at cladogenesis

Per-event weights at cladogenesis
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Per-event weights at cladogenesis

\[ \text{Prob(event|ancestor range)} = \frac{\text{weight}}{\sum \text{weights}} \]
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**Per-event weights at cladogenesis**

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<td>Sympathy (widespread)</td>
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<td>(3-j)/3</td>
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<td>Sympathy (subset)</td>
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<td>Vicariance (narrow)</td>
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<td>Vicariance (widespread)</td>
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<td>(3-j)/3</td>
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<td>Founder</td>
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**Per-event weights at cladogenesis**

\[
\text{Prob(event|ancestor range)} = \frac{\text{weight}}{\sum \text{weights}}
\]

**Per-event weight of founder-event at cladogenesis**
Comparison of DEC and DEC+J: empirical data

• Different Hawaii models for *Psychotria* (Ree & Smith 2008)

• Pacific islands *Cyrtandra* (Clark et al. 2008)

• Northern hemisphere continental *Lonicera* (Smith & Donoghue 2010)
R package:

BioGeoBEARS

TRY IT YOURSELF AT:
http://phylo.wikidot.com/biogeobears
<table>
<thead>
<tr>
<th>Clade +constraints</th>
<th>Model</th>
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<td>DEC DECj</td>
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<td><em>Psychotria</em> - M1</td>
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<tr>
<td><em>Psychotria</em> - stratified</td>
<td>DEC DECj</td>
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Does it matter?

Does model choice affect inference of ancestral geographic ranges?

YES
Hawaiian Islands

Oldest (~5.1 Ma)

Youngest (~0.5 Ma)

K=Kauai
O=Oahu
M=Maui-Nui
H=Hawai‘i
Hawaiian Psychotria, DEC 2-parameter, marginal ML states

DEC inference
Maximum Likelihood states
(global optim)

K=Kauai
O=Oahu
M=Maui-Nui
H=Hawai‘i

http://farm8.static.flickr.com/7446/9252634315_0ecf0ba853_m.jpg

Psychotria hexandra
Hawaiian Psychotria, DEC+J 3-parameter, marginal ML states

DEC+J inference
Maximum Likelihood states (global optim)

K=Kauai
O=Oahu
M=Maui-Nui
H=Hawaii’i

Psychotria hexandra
DEC model - probability of ancestral ranges

K=Kauai
O=Oahu
M=Maui-Nui
H=Hawai‘i

Psychotria hexandra

http://farm8.static.flickr.com/7446/9252634315_0ecf0ba853_m.jpg
DEC+J model - probability of ancestral ranges

Psychotria hexandra

K=Kauai
O=Oahu
M=Maui-Nui
H=Hawai‘i

http://farm8.static.flickr.com/7446/9252634315_0ecf0ba853_m.jpg
Does model choice affect accuracy of ancestral geographic ranges?

YES
Accuracy of ancestral range inference

simulations: DECJ
inference: DEC
average fraction of nodes correct=0.57

simulations: DECJ
inference: DECJ
average fraction of nodes correct=0.87
Example stochastic map

**ML DEC model**

Stochastic map #26/60 under DEC M0 model on Hawaiian Psychotria
anastase: global optim, 4 areas max. dw=0.035; ce=0.028; jw=0; LnL=-34.5420

**ML DEC+J model**

Stochastic map #26/60 under DEC+J M0 model on Hawaiian Psychotria
anastase: global optim, 4 areas max. dw=0; ce=0.114; LnL=-20.9476

(under model M0: no geology)
Biogeographic stochastic mapping in *BioGeoBEARS*

**ML DEC model**

Stochastic map #1/50 under DEC M3 model on Hawaiian Psychotria

- **ML DEC+J model**

Stochastic map #1/50 under DEC+J M3 model on Hawaiian Psychotria

(under model M3: island emergence)
DEC+J advantage is very common...

13 island clades, many under multiple geology models
DEC+J advantage is very common...

13 island clades, many under multiple geology models

Ratio of model weights: DEC+J:DEC
...but, *not* universal:
...but, *not* universal:

*BioGeoBEARS Beer Challenge:*

Find an empirical dataset that does *not* reject DEC
Taygetis butterflies favor DEC

Matos-Maravi et al. (2012), MPE
Papers using BioGeoBEARS (now: about 50 in literature)

Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galiformes: Megapodidae)

Rebecca B. Harris1,2*, Sharon M. Birk2 and Adam D. Leech1,2

Abstract

 Aim: Unique amongst birds, megapodes (family Megapodiidae) have exchanged the strategy of insulating eggs with the warmth of their bodies for incubation behaviour that rely entirely on environmental heat sources. Typically, mound-builders capture heat released from the decomposition of organic materials, while burrow-nesters lay their eggs in geothermal or solar-heated soil. The evolution of this behaviour has led to ecological and physiological adaptations unique to megapodes. Here, we present a phylogeographical approach to resolving the adaptations of all extant megapodes, as well as their biogeographical origins and ancestral nesting behaviour.

Location: Australia.

Methods: We surveyed a phylogeographical approach using 14 species of extant megapodes and estimated divergence times using Bayesian methods. We then estimated migrations and ancestral nesting behaviour using coalescent methods, as well as being influenced by environmental adaptations.

Biogeography of the marmosets and tamarins (Callitrichidae)

Jaece C. Buckner1*, Jessica L. Alfaro2, Anthony B. Rylands4, Michael E. Alfaro1

Abstract

Although marmosets and tamarins are known to be distributed across the Americas, there is a clear geographical separation between species and subspecies, with some species and subspecies being restricted to specific areas, such as the Amazon Basin. This separation is likely due to the environmental conditions of their habitats, such as vegetation density and climate. In this study, we investigated the biogeographical relationships of marmosets and tamarins using a multi-locus phylogenetic approach and compared these results with previous studies to better understand the evolutionary history of these species.
See also:

Matzke (2013), *Frontiers of Biogeography*

Matzke (2014), *Systematic Biology*


But first: The biogeography of...Nick Matzke

Workshops by Nick Matzke

Life track:
- Recent (scheduled)
- Past

Countries visited

Projection: Robinson

Generated with R packages rgdal, geosphere, maptools, sp
Implication #1

FREE YOUR MIND
Implication #1

FREE YOUR MIND

We have a lot of models to explore & test
Implications #2

“All models are wrong, but some models are useful.”

George E. P. Box (1919-2013)
Implications #2

“All models are wrong, but some models are useful.”

-- George Box

I say: we’ll never know the usefulness / misleading qualities unless we do statistical model comparison.
Implication #3

Review by Malte Ebach:

The timely arrival of Tewkesbury Walks acts as an antidote to the extreme reactionary neo-dispersalism of, for example, the recently published The Monkey’s Journey (de Queiroz 2014).

The latter book contends that some cladists foolishly reject dispersal outright. I do not think this is true. These cladists are emphasizing that dispersal is immune to discovery, rather than refuting its existence.


(bold added)
Implication #3

Review by Malte Ebach:

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The latter book contends that some cladists foolishly reject dispersal outright. I do not think this is true. These cladists are emphasizing that dispersal is immune to discovery, rather than refuting its existence.


(bold added)

I suggest: Founder-event dispersal is not immune to discovery. It can be inferred just like anything else with statistical model choice.
Including fossils in biogeography
Results

Ground-truth tree:

Key dates:

1. LCA crown *Canis*: ~4 Ma
2. LCA crown Caninae: ~12 Ma
3. LCA total-group Canidae: ~41 Ma
Results

Slater (2015) analysis: tip+node dates
MrBayes uniform prior

Key dates:
1. LCA crown *Canis*: ~7 Ma
2. LCA crown Caninae: ~22 Ma
3. LCA total-group Canidae: ~41 Ma
Results

Slater (2015) data: tip dates only
MrBayes uniform prior

Key dates:

1. LCA crown *Canis*: ~27 Ma
2. LCA crown *Caninae*: ~36 Ma
3. LCA total-group *Canidae*: ~50 Ma
Results

Slater (2015) data: tip dates only

*BEASTmasterR, BDSS* prior

Key dates:

1. LCA crown *Canis*: ~4 Ma
2. LCA crown *Caninae*: ~12 Ma
3. LCA total-group *Canidae*: ~37 Ma
Results

Slater (2015) data: tip dates only

**BEASTmasterR, SABD**

Key dates:

1. LCA crown *Canis*: ~3 Ma
2. LCA crown Caninae: ~11 Ma
3. LCA total-group Canidae: ~37 Ma
Biogeography of living and fossil Canids (dogs)

Figure 2: Zones used in the biogeographic analysis

N, North America (incl. Central America) - Nearctic
S, South America - Neotropics; E, Palearctic; I, Central / South Asia;
M, North Africa + Arabian peninsula; F, Sub-Saharan Africa

Figure 3: Results of biogeographic analysis of Caninae

Best support values obtained from BioGeoBEARS, DEC+J model, time stratified, 6 areas, global optimal results: d=0.0411; e=0.0268; f=0.0698; LnL=-272.19.

What else can we discover about biogeography?

- with statistical model choice
- on phylogenies
Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
   Founder-event speciation
Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
   - Founder-event speciation
   - Geographic distance
Should distance be important in biogeography?
Historical biogeography: Wallace and Darwin

Wallace (1855): “Every species has come into existence coincident both in space and time with a pre-existing closely allied species.”

Darwin (1859): “the more nearly any two forms are related in blood, the nearer they will generally stand to each other in time and space”.
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For geographers/geostatisticians:

Tobler’s First Law of Geography:

“Everything is related, but closer things are more related.”

— Waldo Tobler
Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
   Founder-event speciation
   Geographic distance
Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
   Founder-event speciation
   Geographic distance
   Environmental distance
The “+x” model: modify dispersal probability by distance^x
New approach: estimate dispersal matrix

Let’s try it.

**Phylogeny:** Zanne et al. (2013), *Nature*, 15,000+ angiosperms

**Geography:** median lat/long of species ranges

**Regions:** Realms x Biomes (58 regions total)

**Assumption:** everything lives in 1 area
Realms x Biomes

606 sp. in a9: Afrotropic
Tropical and Subtropical Moist Broadleaf Forests
1871 sp. in a34: Neotropic
Tropical and Subtropical Moist Broadleaf Forests
Realms x Biomes

701 sp. in a18: Indo–Malay
Tropical and Subtropical Moist Broadleaf Forests
734 sp. in a33: Nearctic
Deserts and Xeric Shrublands
Realms x Biomes

13 sp. in a39: Oceania
Tropical and Subtropical Dry Broadleaf Forests
Model comparison

Base model: BAYAREALIKE-d-e
+a means base rate of dispersal
+x means dispersal prob. modified by distance^x
+n means dispersal prob. modified by environmental distance^n
+J means weight of cladogenetic jump dispersal

Param. LnL
+a -54459.68
Model comparison

Base model: BAYAREALIKE-d-e
+a means base rate of dispersal
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Param. LnL
+a  -54459.68
+a+x -50465.14
Model comparison

Base model: BAYAREALIKE-d-e
+a means base rate of dispersal
+x means dispersal prob. modified by distance^x
+n means dispersal prob. modified by enviromental distance^n
+J means weight of cladogenetic jump dispersal

Param. LnL
+a -54459.68
+a+x -50465.14
+a+x+n -49856.52
Model comparison

Base model: BAYAREALIKE-d-e
+a means base rate of dispersal
+x means dispersal prob. modified by distance^x
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<td>+a+x+n</td>
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## Model comparison

Base model: BAYAREALIKE-d-e

+a means base rate of dispersal

+x means dispersal prob. modified by distance$^x$

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Both distance and environmental distance have big effects on angiosperm dispersal
BioGeoBEARS inference of dispersal events for 14,000 plant species

Figure: Dispersal events between ecoregion centroids, 0.1-1 Ma.
Method: Biogeographical stochastic mapping
Model: BAYAREALIKE+α+distance+environmental distance
Software: BioGeoBEARS (Matzke 2013-2015)
Data: Angiosperm megaphylogeny
(14,000 species from Zanne et al. 2013)
Looking at the global angiosperm macroevolutionary dispersal kernel

Dispersal frequency by geographical distance
Looking at the global angiosperm macroevolutionary dispersal kernel

Great Circle Distance vs. Number of Dispersals

- Distance between area centroids (km)
- Number of dispersal events

- Axes: Log scale
Looking at the global angiosperm macroevolutionary dispersal kernel

Particular transitions (from→to):
Great Circle Distance vs. Number of Dispersals

number of dispersal events for a particular from→to

distance between area centroids (km)
Looking at the global angiosperm macroevolutionary dispersal kernel

Dispersal frequency by environmental distance

Frequency

0 10000 20000 30000 40000 50000 60000

environmental distance (difference in abs(latitude))
Looking at the global angiosperm macroevolutionary dispersal kernel

Environmental Distance vs. Number of Dispersals

- X-axis: difference in abs(latitude) between area centroids
- Y-axis: number of dispersal events
Looking at the global angiosperm macroevolutionary dispersal kernel

Particular transitions (from→to):
Environmental Distance vs. Number of Dispersals

environmental distance between area centroids (abs(latitude))

number of dispersal events
Looking at the global angiosperm macroevolutionary dispersal kernel

Particular transitions (from→to):
Environmental Distance vs. Number of Dispersals

environmental distance between area centroids (abs(latitude))

number of dispersal events
Historical biogeography: Wallace and Darwin

Wallace (1855): “Every species has come into existence coincident both in space and time with a pre-existing closely allied species.”

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We have just seen:

Close relatives tend to have smaller environmental distances (even after geographic distance already accounted for)
In other words...niche conservatism is real.
Studying Ecological Niche Conservatism with Species Distribution Modeling (SDM) / Ecological Niche Modeling (ENM)

1. Fit a niche model
Species locality data + Environmental data layers = Environmental Niche Model (ENM)
Environmental Niche Model (ENM)

Species locality data + Environmental data layers

f(Prob(occurrence))

Temperature

Precipitation

f(Prob(occurrence))
Temperature

f(Prob(occurrence))

Species locality data

Environmental data layers

Precipitation

f(Prob(occurrence))

Ecological niche model

Environmental Niche Model (ENM)
Species locality data + Environmental data layers → Species Distribution Model (SDM)

\[ f(\text{Prob(occurrence)}) \]

\[ \text{Temperature} \]

\[ f(\text{Prob(occurrence)}) \]

\[ \text{Precipitation} \]

Ecological niche model
Ecological Niche Modeling: very popular

Common ENM tools
- BioClim (min/max)
- GLMs
- GAMs
- MaxEnt
- MARS
- RandomForest
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model

2a. Sample from curve:
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model
2a. Sample from curve:

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model
2a. Sample from curve:

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

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Studying Ecological Niche Conservatism with SDM

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2a. Sample from curve:

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model
   2a. Sample from curve:
   
   - **Species 1**
   
   - **Species 2**

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model

2a. Sample from curve:

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model

2a. Sample from curve:

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model

2a. Sample from curve:

Species 1

Species 2

2b. Ancestral states w. Brownian:

Ancestor
Studying Ecological Niche Conservatism with SDM

1. Fit a niche model
2a. Sample from curve:

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

Critiques:
1. Niche curves are inferred estimates, not data
2. Sampling from the curves adds variance
3. No model choice

2b. Ancestral states w. Brownian:
Studying Ecological Niche Conservatism with SDM

Unsolved problem: how are niches homologous?
Studying Ecological Niche Conservatism with SDM

Unsolved problem: how are niches *homologous*?
Studying Ecological Niche Conservatism with SDM

Unsolved problem: how are niches homologous?

![Diagram showing the distribution of species occurrence related to temperature for two species, species 1 and species 2.](image)
Studying Ecological Niche Conservatism with SDM

Unsolved problem: how are niches *homologous*?

![Graphs showing temperature distribution for two species](image)
Another approach: BioClim (limits only)

1. Fit a niche model
Another approach: BioClim (limits only)

1. Fit a niche model

2. Ancestral states w. Brownian:
Another approach: BioClim (limits only)

1. Fit a niche model

2. Ancestral states w. Brownian:
Another approach: BioClim (limits only)

Critiques of the min/max approach:
1. Min/max are inferred estimates, not data
2. Min and max could cross over under Brownian motion
3. No model choice

2. Ancestral states w. Brownian:

![Diagram showing min and max probability distributions for an ancestor.](image)
Homology problem: standard Niche Modelling tools won’t give identical niche models between methods
…or even between random number seeds

Common ENM tools
- BioClim (min/max)
- GLMs
- GAMs
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- MARS
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Homology problem: standard Niche Modelling tools won’t give identical niche models between methods

…or even between random number seeds

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Proposal: PhyloSDM

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\[ \text{logit(Prob(occurrence))} \]

\[ \text{Temperature} \]

Species 1

- optimum
- slope 1
- slope 2

Species 2

- optimum
- slope 1
- slope 2
Proposal: PhyloSDM

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2. Evolve niche parameter(s) with Brownian motion, Ornstein-Uhlenbeck, shifting means, etc.
Models for the evolution of continuous traits

**Brownian Motion**

\[ dX_i(t) = \sigma dB_i(t), \quad t_{i}^{j-1} \leq t \leq t_{i}^{j}. \]

**Orstein Uhlenbeck Process**

\[ dX_i(t) = \alpha (\beta_{i}^{j} - X_i(t)) \, dt + \sigma dB_i(t) \]
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**Brownian motion rate**

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Brownian motion rate
Optimal trait value
Strength of selection (pull to optimum)
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Traditional approach:

(a) Standard ENM (treats species as independent)

Modern day

Stratum with fossil & paleoenvironmental data

Stratum with no fossil/paleoenvironmental data
Traditional approach:  My new approach:

(a) Standard ENM (treats species as independent)  
(b) Proposed joint inference taking into account phylogeny
Conservation paleobiology needs phylogenetic methods

A. Michelle Lawing and Nicholas J. Matzke

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Statistical model choice in phylogenetic biogeography

Outline:

I. Introduction

II. Measuring the importance of:
   - Founder-event speciation
   - Geographic distance
   - Environmental distance
Statistical model choice in phylogenetic biogeography

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I. Introduction

II. Measuring the importance of:
   Founder-event speciation
   Geographic distance
   Environmental distance

III. The future of biogeography: integrating phylogeny, fossils, paleogeography, paleoclimate
My DECRA proposal (funded):
Linking phylogeny to Species Distribution Modelling/Niche Modelling

Traditional approach:
Current methods:

Typical limitations:

Key advance in this DECRA:

Benefits:

Figure 1: Graphical abstract of proposed DECRA research and benefits. Using Bayesian Hierarchical Modelling to combine statistical methods in historical and ecological biogeography will advance scientific understanding of how geography and niche coevolve, and allow improved inference and prediction.

Abbreviations: NG, New Guinea; EA, WA, East & West Australia.
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Current status of phyloSDM

Programmed in JAGS:

- Detection model: $P(\text{detect}|\text{presence})$
- Niche model: $P(\text{presence}|\text{environ, params})$
- Evolutionary model: $P(\text{params}|\text{evo. model})$
- E.g. OU process with shifting means (using a stochastically mapped trait)
- Sample from distrib. of trees, maps

MCMC sampling of possible niche models
Likely advantages of phyloSDM

• Better estimates of ancestral niches
• “Better” estimates of current niches! (“Better” = more robust, less overfitting)
• Perhaps: closer to getting fundamental niche, rather than “accidental” correlates
• Share info: data poor or rare species
• Study niche evolution rates, modes

MCMC sampling of possible niche models
Key challenges

- Scaleability? Minimally, 3 parameters per species per environmental variable +6 evo.
- Interactions between variables
- Is there any way to include the advantages of machine-learning SDM approaches, while maintaining phylogenetic models, hierarchical detection models, etc.

MCMC sampling of possible niche models
Future of biogeography: integration
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(b) Matzke current research

Model inference (BioGeoBEARS)

Phylo-SDMs (carbash)

“Tip-dating” – joint estimation using DNA+traits+fossils (BEASTmaster)

(a) Traditional fields

Historical biogeography

Ecological biogeography

Statistical Phylogenetics

Phylogeny Ranges

Ancestral Range Estimation (ARE)

Species locality data Environmental data layers

Environmental Niche Model (ENM)

Node-dating

Morph. traits: Cladistics

Genomics: Molecular evolution
Future of biogeography: integration

Matzke Research Program:
Combined estimation of evolution of biogeography, niche, traits, molecules

(b) Matzke current research
- Model inference (*BioGeoBEARS*)
- Phylo-SDMs (*carbash*)
- “Tip-dating” – joint estimation using DNA+traits+fossils (*BEASTmasteR*)

(c) Historical biogeography
- Phylogeny
- Ranges
- Ancestral Range Estimation (ARE)

Ecological biogeography
- Species locality data
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- Ecological biogeography
- Statistical Phylogenetics

(e) Practical applications
- Forecasting climate change impacts
- Disease vector modeling
- Pathogen origins and evolution
- Hosts/parasites coevolution

(d) Research applications
- Distance-dependent dispersal models
- Measuring speciation mechanisms
- Measuring speciation
- Measuring dispersal
- Measuring phylo-
- SDMs improved
- Niche evolution & evolvability
- Extinction and invasion
- Trait/biogeography coevolution
- Founder-events and accelerated molecular evolution
- Biogeographical dating

(c) Conservation biology

Future of biogeography: integration
Summary

1. Phylogenies and phylogenetics are fundamental to 21st-century biogeography
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4. Distance — (geographic, environmental), is fundamental and its effect can be estimated
Summary

1. Phylogenies and phylogenetics are fundamental to 21st-century biogeography.
2. Statistical model choice is the way to test general hypotheses in biogeography.
3. Founder-event speciation is important and should be included in models.
4. Distance — (geographic, environmental), is fundamental and its effect can be estimated.
5. PhyloSDM is a step towards integration.
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