Tracking the formation of a species assemblage over time: phylogenetic reconstruction of patterns of colonisation and speciation

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Are species added into an assemblage at an even rate over time?
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A known set of extant taxa that co-exist in a given area
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A known set of extant taxa that co-exist in a given area

Colonisation

In-situ speciation
Are species added into an assemblage at an even rate over time?

Uneven colonization rate due to geographical events
Ali & Huber 2010 Nature

Slow-down in speciation rate due to saturation
Rabosky & Lovette 2008 Proc.R.Soc.B
Approaches to reconstruct patterns of speciation and colonisation
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Use paleontological data

Need continuous fossil record and adequate taxonomic and temporal resolution
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Compare assemblages of known ages

E.g., derive assemblage ages from the formation dates of different islands
Approaches to reconstruct patterns of speciation and colonisation

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   Need continuous fossil record and adequate taxonomic and temporal resolution

Compare assemblages of known ages
   E.g., derive assemblage ages from the formation dates of different islands

Use molecular phylogenies
Sources of error in using molecular phylogenies to infer assemblage history
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Uncertainty in topology and divergence times

A “best” tree is typically used in macroecology study
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   More recent events are more likely to be detected
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Uncertainty in localize speciation and colonization events on a branch
Sources of error in using molecular phylogenies to infer assemblage history

Uncertainty in localizing speciation and colonization events on a node
Sources of error in using molecular phylogenies to infer assemblage history

Uncertainty in localize speciation and colonization events on a node

Where did colonization occur?

outside

inside

inside

outside
Framework of testing assemblage formation using phylogenies

How likely it is to observe the extant species assemblage if it was formed in the way as the null hypothesis predicts?

\[
L \left( \text{assemblage} \mid H_0 \right) = \\
\sum \sum P \left( \text{assemblage} \mid \text{history } i, H_0 \right) \\
\times P \left( \text{history } i \mid \text{phylogeny } j, H_0 \right) \\
\times P \left( \text{phylogeny } j \mid H_0 \right),
\]
Framework of testing assemblage formation using phylogenies

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\[ \times P (\text{history } i | \text{phylogeny } j, H_0) \]
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Topology and time uncertainty
Framework of testing assemblage formation using phylogenies

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\times P \left( \text{history } i \mid \text{phylogeny } j, H_0 \right) \quad \text{Reconstruction uncertainty} \\
\times P \left( \text{phylogeny } j \mid H_0 \right), \quad \text{Topology and time uncertainty}
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Framework of testing assemblage formation using phylogenies

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\[ \times P(\text{history } i \mid \text{phylogeny } j, H_0) \]
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Uncertainty in localizing colonization and speciation

Reconstruction uncertainty

Topology and time uncertainty
Framework of testing even species addition rate using phylogenies

\[ L (\text{assemblage} \mid \text{speciation } \lambda; \text{extinction } \mu; \text{colonization } q_{01}; \text{emigration } q_{10}) = \]

\[ \sum_j \sum_i P (\text{assemblage} \mid \text{history } i; \lambda, \mu, q_{01}, q_{10}) \]

\[ \times P (\text{history } i \mid \text{phylogeny } j; q_{01}, q_{10}) \]

\[ \times P (\text{phylogeny } j \mid \lambda, \mu), \]
Framework of testing even species addition rate using phylogenies

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Joint estimation of topology and divergence time
Framework of testing even species addition rate using phylogenies

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\[ \times P (\text{history} \; i \mid \text{phylogeny} \; j; q_{01}, q_{10}) \quad \text{Continuous-time Markov model} \]

\[ \times P (\text{phylogeny} \; j \mid \lambda, \mu), \quad \text{Joint estimation of topology and divergence time} \]
Framework of testing even species addition rate using phylogenies

\[ L (\text{assemblage} \mid \text{speciation } \lambda; \text{extinction } \mu; \text{colonization } q_{01}; \text{emigration } q_{10}) = \]

\[ \sum_j \sum_i P (\text{assemblage} \mid \text{history } i; \lambda, \mu, q_{01}, q_{10}) \times P (\text{history } i \mid \text{phylogeny } j; q_{01}, q_{10}) \times P (\text{phylogeny } j \mid \lambda, \mu), \]

Birth-death model

Continuous-time Markov model

Joint estimation of topology and divergence time
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Framework of testing even species addition rate using phylogenies

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Birth-death model

\[ f(t \mid n) = \lambda^{n-1} (\lambda - \mu - q_{10})^2 \frac{(1 - e^{-(\lambda - \mu - q_{10})t})^{n-1} e^{-(\lambda - \mu - q_{10})t}}{(\lambda - \mu e^{-(\lambda - \mu - q_{10})t})^{n+1}} \int_0^T \frac{f(t)}{p(t \mid n) f(t) dt} \]
Framework of testing even species addition rate using phylogenies

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**Birth-death model**

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$$f(t) = [(q_{10} + q_{01} e^{(q_{10}+q_{01})(t-T)})q_{01}] N_0(t)$$
Framework of testing even species addition rate using phylogenies

\[ L \left( \text{assemblage} \mid \text{speciation} \, \lambda; \, \text{extinction} \, \mu; \, \text{colonization} \, q_{01}; \, \text{emigration} \, q_{10} \right) = \sum \sum \sum P \left( \text{assemblage} \mid \text{history} \, i; \, \lambda, \, \mu, \, q_{01}, \, q_{10} \right) \]

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\[ f(t) = \left[ (q_{10} + q_{01} e^{(q_{10} + q_{01})(t-T)}) q_{01} \right] N_0(t) \]

\[ N_0(t) \text{ is constant in macroecology study} \]

\[ N_0(t) \text{ follows deterministic two state birth-death model in macroevolution study} \]
Framework of testing even species addition rate using phylogenies

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### Diagram

![Diagram showing speciation and colonization events with time points \( t_1 \) and \( t_2 \).]
Framework of testing even species addition rate using phylogenies

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**Birth-death model**

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f(s \mid t) = \frac{(\lambda - \mu - q_{10})^2 e^{-(\lambda - \mu - q_{10})s}}{[\lambda - (\mu + q_{10})e^{-(\lambda - \mu - q_{10})s}]^2} \frac{\lambda - (\mu + q_{10})e^{-(\lambda - \mu - q_{10})t}}{1 - e^{-(\lambda - \mu - q_{10})t}}
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Or, for genus-level phylogeny

\[ f(s \mid t) = \left[\frac{1 - e^{-(\lambda - \mu - q_{10})s}}{\lambda - (\mu + q_{10})e^{-(\lambda - \mu - q_{10})s}} \frac{\lambda - (\mu + q_{10})e^{-(\lambda - \mu - q_{10})t}}{1 - e^{-(\lambda - \mu - q_{10})t}}\right]^{n-1} \]
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Prior \( f(s) \) follows coalescent theory if using species tree approach
Taxon sampling bias is inevitable: Compare simulated and observed phylogenies
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Step 1: MCMC searches for likely sets of parameter values
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Step 2: Simulate phylogenies using those parameter sets
          Constrain the extant number of lineages and total divergence time
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Step 3: ML (observed) <= ML(simulated)?
small type I error, large type II error
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Constrain the extant number of lineages and total divergence time

Step 3: ML (observed) << ML(simulated)?
small type I error, large type II error

Step 4: Construct CI of simulated and observed histories:
Colonization frequency over time
Number of extant lineages per colonization
Madagascar squamates

New Zealand passerines

Crottini et al.
2012 PNAS
Madagascar squamates

New Zealand passerines

Include all the taxa in the assemblage

Include the closest relatives of each taxon outside the assemblage

Crottini et al. 2012 PNAS
More colorizations during Cenozoic Era in Madagascar squamates

\[ P \left( L_{\text{sim}} \leq L_{\text{obs}} \right) = 0.49 \]

Colonization frequencies over time

Frequency distribution of number of extant species per colonization
**Constant colonization but inconstant speciation in New Zealand passerines**

\[ P(\text{\textit{L}}_{\text{sim}} \leq \text{\textit{L}}_{\text{obs}}) = 0.04 \]

Colonization frequencies over time

Frequency distribution of number of extant species per colonization

**Excess of single colonizing lineage**
Type I error estimated by simulations

Apply the method to 100 simulated phylogenies, each with 100 slice sampling to search for likely parameter sets
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Likelihoods: 0
Comparisons of reconstructed histories: 0.1
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Sample size?
MCMC sampling?
Type II error?
Further explore taxon sampling bias

The method does not reconstruct unbiased assemblage histories. Thus, it should not be used to test effects of a specific historical or geological events.
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A hidden Markov model may reconstruct a less biased assemblage history. Require numerical integrations and time-consuming.
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Compare performance between hidden Markov methods and our analytical approach in reconstructing assemblage histories.
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